VOCAL COMBINATIONS IN GUENON COMMUNICATION

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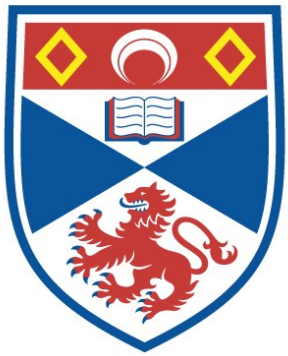

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Camille Coye

Prepared at the UMR 6552 EthoS in Rennes and the School of Psychology of St Andrews

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VOCAL COMBINATIONS IN GUENON COMMUNICATION

PhD viva held in Paimpont, on the 5th July 2016

in front of the following committee:

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CHAPTER 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

1.1. Flexibility and combinatorial capacities as central keys of the theories on the origins of human language

Human language is a unique communication system, relying on a complex set of communicative and cognitive capacities. Acquiring a spoken language requires capacities of flexible vocal production but also involves complex rules of combination and hierarchical organisation that allow to create meaning. These elements are the cornerstones of language generativity, giving rise to an infinite number of messages. In spite of decades of intensive research conducted by specialists from various fields, the debate about the origins and evolution of language remains open (Lemasson, 2011; Scott-Phillips, 2015), opposing two main schools of thoughts.

1.1.1. Discontinuist theory

This theory supports the existence of a qualitative gap between human language and animal communication (Bickerton, 2009). In particular, if discontinuists admit that some abilities required for (but not restricted to) language exist in animals, these authors also support the idea that some essential characteristics of language are uniquely human such as semantic symbols (*i.e.* symbolic mental representation related to a word; Deacon, 1998, p. 19) and recursion (*i.e.* a structure that refers to itself or a structure that includes a structure of the same kind embedded inside it; Bickerton & Szathmáry, 2009; Chomsky, 1981, p. 198). Hauser, Chomsky and Fitch (2002) hence proposed to distinguish between the components of the faculty of language in its broad sense (FLB) which implies a variety of communicative and cognitive processes not limited to humans, and the faculty of language in its narrow sense (FLN) which comprises only

the computational mechanisms of recursion and which they consider to be unique to our species.

1.1.2. Continuist theories

Continuist theories of human language support the idea that language evolved on the basis of pre-existing cognitive and communicative capacities that we might share with other animal species. Hence, they place the difference between humans and animals at a quantitative rather than qualitative level. These theories are supported by the presence of language-like capacities (*i.e.* functionally or structurally affiliated to characteristics of language) in animals but the sensory modality primarily involved in the development of language-like abilities in our ancestors remains the topic of debates.

1.1.2.1. Theory of the gestural origin of language

This theory proposes that human language might have evolved initially via the development of gestural communication. The rationale behind this theory is based firstly on the close association between speech and gestures in humans both in terms of spontaneous production (McNeill, 1985), language acquisition in children (Bates & Dick, 2002) and neural structures involved in the processing of spoken and sign language (Petitto et al., 2000). Furthermore, if non-human primates lack flexibility in terms of vocal production (see paragraph 1.2 below), they can produce gestures relatively flexibly without facing physical limitations and our ancestors might have been in the same situation (Tomasello & Call, 2007). The gestural theory of language evolution is notably supported by the flexible use of gestures by non-human primates in various contexts (Liebal, Pika, & Tomasello, 2004; Pika, Liebal, Call, & Tomasello, 2005). In particular, increased activation in the brain left hemisphere resembling the one observed in humans (Kimura, 1973) was highlighted during the emission of

communicative gestures (as opposed to non-communicative manual actions) in apes (Hopkins & Leavens, 1998; Meguerditchian, 2009; Taglialatela, Russell, Schaeffer, & Hopkins, 2008), and monkeys (Meguerditchian, Molesti, & Vauclair, 2011; Meguerditchian & Vauclair, 2006). In addition, authors found evidence for flexible use and progressive ritualization of gestures between social partners (Pika et al., 2005; Pika, Liebal, & Tomasello, 2003; Tomasello et al., 1997), as well as evidence for intentional use of some gestures in non-human primates. The latter were based on criteria like persistence and elaboration of signals produced until the desired outcome is reached (Leavens, Russell, & Hopkins, 2005) or sensibility to the presence and attentional state of an audience (Call & Tomasello, 1994; Cartmill & Byrne, 2007; Kaminski, Call, & Tomasello, 2004; Maille, Engelhart, Bourjade, & Blois-Heulin, 2012). For some of the authors supporting this theory, another reason why human language may not find its roots into vocal communication comes from the idea that nonhuman primate calls would be purely emotional utterances that would rather relate to human emotional oral emissions such as laughter and cry (Corballis, 2003; Deacon, 1997).

1.1.2.2. Theory of the vocal origin of language

This second school of thoughts defends the theory of a progressive evolution of language from vocal communication. The rationale being that there is more than just laughing and crying in nonhuman primate calling (Lemasson, 2011). This theory is firstly supported by the remarkable capacities of call perception displayed by non-human primates, including categorical perception of graded variation in call structure (Fedurek & Slocombe, 2011; Fischer, 1998; Fischer, Cheney, & Seyfarth, 2000; May, Moody, & Stebbins, 1989), the ability to assign meaning to calls and to call combinations (Arnold & Zuberbühler, 2008; Schel, Candiotti, & Zuberbühler, 2010; Zuberbühler, 2000a), and to make decisions based on additional contextual cues (Arnold & Zuberbühler, 2013; Palombit, Seyfarth, & Cheney, 1997). Secondly, although

call emission is certainly less flexible than the production of gestures in monkeys and apes, it is less rigid than initially thought, in terms of both call structure and (even more) use. Several language-like properties have been described in nonhuman primate vocal communication: socially-determined variations in call structure (Lemasson, Jubin, Masataka, & Arlet, 2016; Lemasson, Ouattara, Petit, & Zuberbühler, 2011; Mitani & Gros-Louis, 1998; Watson et al., 2015), vocal innovation (Hopkins, Taglialatela, & Leavens, 2007; Ouattara, Zuberbühler, N'goran, Gombert, & Lemasson, 2009), conversational rules such as call overlap avoidance and turn-taking (Chow, Mitchell, & Miller, 2015; Lemasson et al., 2011; Lemasson, Guilloux, Barbu, Lacroix, & Koda, 2013), referentiality (Caesar & Zuberbühler, 2012; Kirchhof & Hammerschmidt, 2006; Zuberbühler, 2000b), and intentionality. The latter was suggested based on criteria like audience effects (Di Bitetti, 2005; Hostetter, Cantero, & Hopkins, 2001; Slocombe & Zuberbühler, 2007; Townsend & Zuberbuhler, 2009), persistence and elaboration (Koda, 2004), and sensibility to the reaction and state of knowledge of receivers (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013).

Globally, although the theories presented above propose distinct evolutionary scenarios, all authors acknowledge the importance of comparative studies with animals to shed light on the evolution of communication in the human lineage and beyond (Fedurek & Slocombe, 2011; Hauser et al., 2002; Lemasson, 2011; Meguerditchian, Cochet, & Vauclair, 2011). In line with this, authors supporting both theories explored and revealed various examples of flexible use, learning, referential and intentional production that participate in building parallels between human language and animal communication. However, the existence of vocal combinatorial abilities in non-human primates, one essential feature of human language, remains a central element in the debate about the evolution of language. The question of whether humans are the

only primates able to combine gestures or calls in a predictable and meaningful way is the subject of current vivid discussions (Lowenthal & Lefebvre, 2013). Apes often use gestures in long bouts, which sequences often includes repetitions of the same gesture (Liebal, Call, & Tomasello, 2004; Tanner, 2004). But the repetition or the insertion of alternative gestures did not seem associated with changes in the "message" or efficiency of the sequence and rather appeared as a result of recipient's lack of responsiveness (Genty & Byrne, 2010; Hobaiter & Byrne, 2011; Liebal, Call, et al., 2004). Hence, although this may only reflect a lack of detailed studies in monkeys, sequences of gestures seem limited to apes. On the contrary, combinatorial mechanisms are widespread in the vocal communication of non-human primates (see section 1.3 of this chapter) and more broadly, in the communication of various animal species. They have been under the focus of interest of scientists for decades and might offer a path to shed light on the development of a hierarchical organisation of language in our species.

1.1.3. Vocal communication and combinatorial abilities in animals

Combination of vocal units are commonly reported in animals from various taxa that can merge acoustic units (*i.e.* basic element consisting of a continuous mark on a sonogram, also termed notes in birds) into complex calls (*e.g.* consisting of several units merged linearly with no or very short silence between them, also termed motifs in birds). These call units and complex calls can then also be combined in call sequences (*i.e.* series of calls uttered in sequence and separated by a silent interval always shorter than silent gaps between sequences, also termed song in birds) (Berwick, Okanoya, Beckers, & Bolhuis, 2011; Bohn, Schmidt-French, Ma, & Pollak, 2008; ten Cate & Okanoya, 2012).

Birds are likely one of the most famous example as birdsong is an historical model for studies of parallels between human language and animal communication (Bremond, 1968; Kroodsma,

1977; Kroodsma & Miller, 1996; Marler, 1976). Many bird species display a remarkable vocal flexibility, involving progressive learning of song patterns under the influence of social interactions with a 'demonstrator' and auditory feedback (Konishi, 1965; Marler, 1970; Price, 1979; Thorpe, 1958). Although the number of notes in the repertoire of birds is very variable and ranges from less than five (*e.g.* in red-billed firefinch (*Lagonosticta senegala*) or in short-toed treecreeper (*Certhia brachydactyla*) ; Bremond, 1968, p. 121) to more than a hundred elements (*e.g.* Northern mockingbird (*Mimus polyglottos*) Gammon & Altizer, 2011), birdsong often involves the combination of varied notes into 'motifs' and long sequences with variable levels of complexity (Berwick et al., 2011). Amongst other examples, we could cite winter wrens (*Troglodytes troglodytes*) (Kroodsma, 1977), Bengalese finches (*Loncura striata*) (Honda & Okanoya, 1999), mockingbirds (Gammon & Altizer, 2011), European starlings (*Sturnus vulgaris*) (Hausberger, 1990), several species of chickadees (Hailman & Ficken, 1986; Lucas & Freeberg, 2007), and blue-throated Hummingbirds (*Lampornis clemenciae*) (Sigler Ficken, Rusch, Taylor, & Powers, 2000) which ability to combine call units following a non-random temporal pattern was studied in details.

In addition, several species of mammals also use complex vocal structures involving the combination of call units into complex calls and/or call sequences (named as 'song' or 'vocal sequence' depending on the species considered). Marine mammals are renowned for their remarkable vocal plasticity and complex singing behaviour, that allows underwater communication over large distances (humpback whales (*Megaptera novaeangliae*): Au et al., 2006; Payne & McVay, 1971; Killer whales (*Orcinus orca*): Riesch, Ford, & Thomsen, 2008, 2006; pilot whales (*Globicephala sp.*): Tyack, 1998). These sequences often respond to specific organisation patterns, and examples of dialectal variations were reported in the temporal organisation of click and whistle sequences of sperm whales (*Physeter microcephalus*) and killer whales (Deecke, Ford, & Spong, 2000; Riesch et al., 2006; Weilgart & Whitehead, 1997).

Furthermore, other species from taxa less renowned for the complexity and plasticity of their vocal communication also display vocal systems involving call combination. Several studies reported call combination in monkeys (*e.g.* Campbell's monkeys (*Cercopithecus campbelli*): Ouattara, Lemasson, & Zuberbühler, 2009b, 2009c; cotton-top tamarins (*Saguinus Oedipus*): Cleveland & Snowdon, 1982; and apes (various gibbons species: Clarke, Reichard, & Zuberbühler, 2006; Mitani, 1987; Mitani & Marler, 1989; bonobos (*Pan paniscus*): Clay & Zuberbühler, 2009; Gorillas (Gorilla sp.): Hedwig, Hammerschmidt, Mundry, Robbins, & Boesch, 2014, orangutans (*Pongo sp.*): Lameira et al., 2013; see section 1.3 of this chapter) as well as in other terrestrial mammals. For instance, rock hyraxes (*Procavia capensis*) give long song bouts that relate notably to caller's body size, social status and hormonal state and display dialectal variations in sequence organisation (Kershenbaum, Ilany, Blaustein, & Geffen, 2012; Koren & Geffen, 2009). Several species of bats also display complex sequences which organisation seems to possess structural consistencies (*i.e.* mustached bats (*Pteronotus parnellii*): Kanwal, Matsumura, Ohlemiller, & Suga, 1994; free-tailed bats (*Tadarida brasiliensis*): Bohn et al., 2008; Bohn, Schmidt-French, Schwartz, Smotherman, & Pollak, 2009; sac-winged bats Behr & von Helversen, 2004). Finally, the *Herpestidae* family also counts several species using combined structures to various extents and notably species using combined calls which structure is meaningful to receivers (*e.g.* meerkats (*Suricata suricatta*) and banded mongooses (*Mungos mungo*): Jansen, Cant, & Manser, 2012; Manser et al., 2014).

A high number of studies describing combinatorial patterns in animals used terms borrowed from the vocabulary of linguistics such as 'syntax' (Holland, Dabelsteen, & Paris, 2000; Honda & Okanoya, 1999), 'phrase' (Bohn et al., 2008), 'syllable" (Bohn et al., 2009; Cleveland & Snowdon, 1982) or 'phonology' (Nowicki, Searcy, Hughes, & Podos, 2001). However, the comparative approach with language was not taken much further in most cases as the original, linguistic, definitions of those terms had not always much to do with the structures and concepts

labelled by the same terms in animals (but see section 6.4 for a discussion). This thesis proposes to investigate more deeply the combinatorial features of the communication systems described in some non-human primates using a more rigorous comparative approach with language. At this stage, it must be clearly stated that we do not aim at demonstrating 'precursors' of language in the sense of homologous mechanisms inherited from a common ancestor. Indeed, addressing this point would require both a comprehensive understanding of these mechanisms in non-human primates and a larger-scale data about the presence of such capacities across the primate lineage, notably in great apes. Vocalisations of non-human primates have long been considered as strongly stereotypic with only little acoustic plasticity. More recently, it has been proposed that call combination might allow them to face important communicative needs and diversify their vocal repertoires in spite of strong articulatory constraints (Arnold & Zuberbühler, 2008; Zuberbühler & Lemasson, 2014). Here, we propose to investigate the nature of the combinatorial mechanisms in non-human primates as well as their possible functions at the ultimate level before drawing hypotheses about their possible evolution.

1.2. Articulatory constraints in non-human primates: a limit of call diversification?

1.2.1. Mechanisms of vocal production in human and non-human primates

1.2.1.1. Vocal apparatus

According to the source-filter theory (Fant, 1960), the production of vocalisations is a two-stage process during which a sound is initially produced when an air flow circulating from the lungs through the larynx sets vocal folds into vibration. This sound is then filtered when passing by the supralaryngeal vocal tract and, mostly in humans, further 'shaped' by the articulatory system (Titze & Martin, 1998). Human and non-human primates possess globally similar vocal apparatus (Fitch, 2002) which involve four main components: the respiratory system composed of the lungs, trachea, and associated muscles (*e.g.* diaphragm); the phonation system composed

of the larynx and vocal folds; the resonance system which involves the supralaryngeal vocal tract composed of the nasal, oral and pharyngeal cavities and the articulatory system composed of the tongue, lips, jaws, palate and teeth (Titze & Martin, 1998).

Two main anatomical differences distinguish human from non-human primates. Firstly, some non-human primates possess air-sacs, which serve to amplify and lower pitch of calls (Gautier, 1971) and have been lost in our hominid ancestors (Fitch, 2000a; Nottebohm, 1976). The exact function of these extra-laryngeal structures remains unclear (Hewitt, MacLarnon, & Jones, 2002), but they are unlikely relevant to explain difference in vocal control between human and non-human primates (Lieberman, 2007). Secondly, larynx's resting position is much lower in humans (where it stands in the oral cavity), compared to non-human primates (where larynx stands in the nasal cavity) (Negus, 1949). This observation was conducted on dead individuals and initially led authors to hypothesize that the higher larynx position in animals limits their phonation and explains partly the discrepancies between human and animal's vocal production as the increased pharynx size in humans might allow an improved tongue mobility (Lieberman, Crelin, & Klatt, 1972; Lieberman, Klatt, & Wilson, 1969). But more recent studies, allowing the dynamic visualisation of animals' vocal tract during phonation, showed that several mammals including non-human primates lower the position of their larynx when vocalizing (Fitch, 2000b). Although the lower larynx might have evolved in humans to facilitate speech production, it does not constitute an exclusive explanation for humans' unique phonation (Fitch & Reby, 2001).

Vocalisations' structure is shaped jointly by all the organs involved in phonation. The temporal characteristics of the call (*i.e.* duration, rate) and its amplitude depend on the respiratory system (*i.e.* duration, "rhythm" and speed of air flow). The rate at which the vocal folds vibrate determines the fundamental frequency of the sound (F0, the lowest frequency of the vocalisation) and harmonics (*i.e.* integer multiples of F0). The energy distribution of the sound

and notably the formants (*i.e.* concentration of acoustic energy at particular frequencies) are determined by the structure of the "filter" which attenuate some frequencies while leaving others relatively intact (Briefer, 2012). Several recent studies suggest that the core difference distinguishing humans from other primates in terms of vocal production lie in the neuroanatomical structures underlying the voluntary control of respiratory, laryngeal and supralaryngeal organs of phonation.

1.2.1.2. Neuroanatomical structures and voluntary control of phonation

Two cerebral systems are involved in the production and control of vocalisations. The first one is common to all mammals and includes subcortical structures from the limbic system, notably the periaqueductal grey (Fitch, 2006; Ploog, 2004). This system is involved in the production of vocalisations in relation with caller's emotional state and notably supports the emission of laughter in humans (Jurgens & Ploog, 1981; Ploog, 2004).

The second system appeared more recently and involves cortical structures and in particular a direct link between the motor cortex and various motor nuclei (which contain the nuclei of motor neurons; Jürgens, 1998; Ploog, 2004). This corticomotoneural pathway allows a fine-tuned, voluntary control of movements and an improved control of the articulators (*e.g.* tongue, lips, jaws, palate; Hepp-Reymond, 1988; Ploog, 2004) and larynx as a consequence of the direct link between the motor cortex and motor nuclei participating in the control of these structures (*i.e.* respectively the hypoglossal nucleus and the nucleus ambiguous; Fitch, 2006; Jürgens, 1998). It developed in the primate lineage (*e.g.* direct connections between the motor cortex and the hypoglossal nucleus are absent in non-primates as tree shrew, but tamarins possess a few fibres linking these structures and rhesus macaques possess more) to reach its peak in humans (Chen & Jürgens, 1995). The important development of this second system in

humans likely plays an important role in the voluntary and precise control that humans possess over their vocal production (Coudé et al., 2011; Ploog, 2004).

In addition to this major shift in brain organisation, two additional peripheral differences might allow an increased vocal control in humans compared to non-human primates. The first one also involves the structures controlling the articulators: humans possess a larger hypoglossal canal than chimpanzees and gorillas (Kay, Cartmill, & Balow, 1998). This canal conducts the motor fibres that innervate the tongue and the authors proposed that its larger diameter in humans indicates a better articulatory control which would result from a better innervation of the tongue (Kay et al., 1998). The second difference concerns the increased respiratory control that humans demonstrate compared to other primates that may result, at least partly, from an increased diameter of the thoracic vocal canal which conducts motor neurons of intercostal and abdominal muscles (MacLarnon & Hewitt, 1999).

Finally, humans differ strikingly from their non-human counterparts in regards of their impressive capacity of vocal learning and imitation that are essential during the acquisition of speech (Fitch, 2000a). Clinical research on genetically transmitted disorders shed light on this particularity of humans among primates by identifying a now famous gene: FOXP2 (Hurst, Baraitser, Auger, Graham, & Norell, 1990). This gene encodes a transcription factor (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001) that plays a central role during foetal development of cerebral circuits in humans and many other vertebrate species (Ferland, Cherry, Preware, Morrisey, & Walsh, 2003; Lai, Gerrelli, Monaco, Fisher, & Copp, 2003; Takahashi et al., 2015). These circuits are important for learning and production of speech sequences in humans (Watkins, Dronkers, & Vargha-Khadem, 2002) and more generally in production of vocalisations including complex combinatorial patterns of movements in animals and notably vocal learning in birds (Enard et al., 2009; Haesler et al., 2007; Jarvis, 2004; Scharff & White, 2004). Due to its crucial role in brain development, this gene's structure and patterns of

expression have been highly conserved among vertebrates (see Fisher & Marcus, 2006 for a review) but its sequence has undergone important changes after the split between the human branch and chimpanzees (Enard et al., 2002). To conclude, we may say that FOXP2 seems to have acquired this derived function in humans on the basis of its 'historical' function in vertebrates and likely took part in the evolution of humans' linguistic capacities although this gene alone is not sufficient to explain the gap between humans and other animal species (Fisher & Marcus, 2006).

The information reviewed in this section shed light on the neuroanatomical structures responsible for the contrasting capacities of fine-tuned voluntary control and vocal learning observed in humans and non-human primates. But, if humans obviously control their vocal production to a much larger extent than other primates, one can legitimately wonder about the extent to which non-human primates do (or do not) display flexible vocal production.

1.2.2. Flexibility and its limits in the vocal behaviour of non-human primates

1.2.2.1. Limited flexibility in call production

As the first neural circuits underlying vocal production discovered in non-human primates were subcortical, limbic-related systems, we initially thought that non-human primates' vocalisations did not depend on any kind of voluntary control but consisted in purely emotional reactions (Coudé et al., 2011; Ghazanfar & Eliades, 2014; Hage & Nieder, 2013; Jürgens, 1995). This hypothesis was notably supported by experiments showing that the electric stimulation of some brain areas, notably the periaqueductal grey, suffices to trigger species-specific vocalisations (Fichtel, Hammerschmidt, & Jürgens, 2001; Jürgens, 1998; Jurgens & Ploog, 1981; Newman, 2007).

In addition, a general consensus was that non-human primates' vocal repertoires were fixed and composed of a genetically determined set of calls. These ideas were supported by early observations demonstrating that animals that never heard conspecifics could acquire the species' specific normal vocalisations such as deaf animals (Talmage-Riggs, Winter, Ploog, & Mayer, 1972 but see Egnor & Hauser, 2004; Roupe, Pistorio, & Wang, 2003), infants raised by mute or heterospecific mothers or in social isolation (Boutan, 1913; Hammerschmidt & Fischer, 2008; Hammerschmidt, Freudenstein, & Jürgens, 2001; Owren, Dieter, Seyfarth, & Cheney, 1992; Winter, Handley, Ploog, & Schott, 1973). Additional hybridization experiments further confirmed the importance of genetic determinism in non-human primates' vocal repertoire as the vocalisations produced by hybrid offspring displayed some genetically determined characteristics that showed influence from both parental species (Geissmann, 1984). In line with this, the structure of vocal signals is often relatively well conserved in closely related species and even allows to retrace the phylogenetic relationships between species (Gautier, 1988; Geissmann, 1984, 2002; Meyer et al., 2012). Finally, the few unsuccessful yet conclusive attempts to teach articulated speech to home-raised chimpanzees (Hayes & Hayes, 1951; Kellogg, 1968), while specimens of the same species were able to acquire (to a limited extent) sign language (Gardner & Gardner, 1969; Rumbaugh, Von Glasersfeld, Warner, Pisani, & Gill, 1974), firmly confirmed the gap between humans and non-human primates in terms of vocal production.

These observations constitute a strong line of evidence supporting the idea that non-human primates lack control over signal's acoustic structure and more broadly over voluntary call production. This is undoubtedly true to a certain extent, and easily understandable as we can imagine that inefficient calling behaviour in urgent contexts (*e.g.* predator attacks or infants distress) is susceptible to have dramatic consequences. Hence, we could expect that calls associated with situations in which a 'mistake' resulting from individuals' inexperience would

be lethal get under strong innate and genetic determinism. Nevertheless, if stereotypic call's structure and limited voluntary control can be advantageous in some occasions and likely play a part in non-human primates' communication, such limits may also have severe drawbacks, notably when it comes to dealing with a changing environment, including complex and dynamic social relationships.

1.2.2.2. But yet some vocalisations are not entirely inflexible

The previous paragraph reviewed findings suggesting that non-human primates (1) lacked voluntary control over their vocal production and (2) possessed pre-determined vocal repertoires composed of acoustically stereotypic calls. The studies reviewed in this section nuance those assertions by demonstrating cases of flexible vocal production (*i.e.* capacity to alter the acoustic structure of calls).

1.2.2.2.1. Flexible acoustic structures

Evidence for some vocal flexibility notably comes from studies of infant's vocal ontogenesis which revealed cases of babbling in pygmy marmosets (*Cebuella pygmaea*) (Elowson, Snowdon, & Lazaro-Perea, 1998a, 1998b; Snowdon & Elowson, 2001) and common marmosets (*Callithrix jacchus*) (Pistorio, Vintch, & Wang, 2006) involving the production of structures that differed from the 'normal' adult production. But, variation in calls' structure also occur in adults and has logically been more documented than in infants (Egnor & Hauser, 2004). In particular, evidence for variation in calls' acoustic structure as a function of caller's arousal and social life have been reported.

i. Arousal-driven acoustic variability

Authors could identify vocal correlates of valence of the situation and caller's arousal. Valence will require more research effort and could not be associated with systematic vocal alterations but might vary with call duration (decreasing in positive contexts) and variations in call's fundamental frequency, although it differs depending on the taxa studied (see Briefer, 2012 for a review). Arousal, which has been more extensively studied, is associated with longer (Fichtel et al., 2001; Rendall, 2003) and louder (Fichtel & Hammerschmidt, 2002, 2003; Yamaguchi, Izumi, & Nakamura, 2010) vocalisations, given at faster rates (Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010; Norcross & Newman, 1999) and with higher frequencies (Fichtel & Hammerschmidt, 2002, 2003; Norcross & Newman, 1999; Schrader & Todt, 1993; Slocombe & Zuberbühler, 2007; Sugiura, 2007). Interestingly, the effects of arousal on call's structure seem to be remarkably consistent across primate species (Lemasson, Remeuf, Rossard, & Zimmermann, 2012) and notably between human and non-human primates (Briefer, 2012). In line with this, authors could identify "acoustic profiles" that correlate with distinct emotional states in humans and were consistent across populations and languages (Hammerschmidt & Jürgens, 2007; Pell, Paulmann, Dara, Alasseri, & Kotz, 2008). The transversal effect of arousal on calls' structure was further confirmed by studies showing cross-cultural and cross-language recognition of speaker's emotions (Sauter, Eisner, Ekman, & Scott, 2010; Scherer, Banse, & Wallbott, 2001), as well as interspecific (human – monkey) assessment of caller's emotional state based on acoustic cues (Leinonen, Hiltunen, Linnankoski, & Laakso, 1997). The consistence and prevalence of such alterations in call's acoustic structure as a function of caller's emotional state in most mammals (Briefer, 2012) suggest that this is a phylogenetically ancient and remarkably well-conserved characteristic (Lemasson et al., 2012). By providing cues about caller's emotional state, it allows receivers to anticipate its reactions and likely plays an important role in regulation of social relationships and interactions, as confirmed by the

studies highlighting the relevance of such emotion-related variations to receivers (Slocombe & Zuberbühler, 2005; Slocombe, Townsend, & Zuberbühler, 2009; Zimmermann, Leliveld, & Schehka, 2013).

ii. Socially-driven acoustic variability

Differences in the acoustic structure of non-human primate affiliative vocalizations have been reported both between groups of individuals and within the calls of individuals. The former are often termed 'dialects' and we will purposely overlook the examples in which these differences could be attributed to genetic or habitat-related differences (*e.g.* Delgado et al., 2009), to focus on the cases suggesting the existence of socially-guided variations. Such differences in call's acoustic structure between-groups, which could not be explained by genetic divergence or habitat differences, exist in Japanese macaques (*Macaca fuscata*) (Tanaka, Sugiura, & Masataka, 2006), grey mouse lemurs (*Microcebus murinus*) (Hafen, Neveu, Rumpler, Wilden, & Zimmermann, 1998), chimpanzees (Crockford, Herbinger, Vigilant, & Boesch, 2004; Marshall, Wrangham, & Arcadi, 1999) and cotton-top tamarins (Weiss, Garibaldi, & Hauser, 2001). In this latter case twin males housed separately uttered calls that differed more from each other than from calls of other members of their respective groups.

In addition, several studies reported modifications of the acoustic structure of calls at the individual level, as a function of caller's social relationships. Acoustic convergence (defined in regards of analogous work in birds: Brown & Farabaugh, 1997) occurs when an individual matches the frequency contours of its calls to those given by others. This phenomenon can take the form of 'long-term vocal convergence' between preferential partners. It was described in pygmy marmosets in which newly paired individuals progressively adjust the acoustic structure of their calls to each other (Snowdon & Elowson, 1999) and in newly paired siamangs'

(*Hylobates syndactylus*) duets (Geissmann, 1999). Similarly, food calls given by chimpanzees settled in a new group converged gradually towards the acoustic structures used by their new group members after the development of affiliative relationships (Watson et al., 2015). Wied's black tufted-ear marmosets (*Callithrix kuhlii*) also modified the structure of their phee call in response to changing social conditions (*i.e.* new neighbours; Rukstalis, Fite, & French, 2003). Furthermore, authors showed that female Campbell's monkeys shared call variants (*i.e.* stereotypic call structure used consistently over long periods of time, up to four variants per female and per year, Lemasson & Hausberger, 2004) with one or several preferential social partners. The pattern of vocal sharing reflected the social dynamic of the group (Lemasson, Gautier, & Hausberger, 2003; Lemasson & Hausberger, 2004), and further studies on wild Campbell's monkeys showed that acoustic similarity between females was correlated with indices of social affiliation (*i.e.* time spent grooming and in close spatial proximity) but not with an index of genetic relatedness (Lemasson et al., 2011). Importantly, the frequency contours were perceptually relevant to the females as they discriminated between variants currently used in the group and older variants no longer uttered normally by females (Lemasson, Hausberger, & Zuberbühler, 2005). Also, a recent study on Japanese macaques showed that low-ranking females seemed to converge vocally towards the calls of dominant females (Lemasson et al., 2016).

In addition, vocal convergence also occurs on a shorter timescale when an individual matches momentarily the structure of its call to those of other individuals it is interacting with. Such cases of 'short-term vocal convergence' were described in Japanese macaques (Sugiura, 1998), chimpanzees (Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998), Diana monkeys (*Cercopithecus diana*) (Candiotti, Zuberbühler, & Lemasson, 2012b) and agile gibbons (*Hylobates agilis agilis*) (Koda, Lemasson, Oyakawa, Pamungkas, & Masataka, 2013).

Hence, in spite of neuroanatomical characteristics imposing strong articulatory constraints on the vocal production of non-human primates, these animals display, to some extent, acoustic flexibility. Interestingly, several cases of acoustic variations among those cited above appeared to be relevant to receivers (Lemasson et al., 2005; Slocombe et al., 2009; Zimmermann et al., 2013), and several others are likely to be so as non-human primates' capacity to perceive and discriminate subtle acoustic cues largely overcomes their production capacities (Seyfarth & Cheney, 2010).

Importantly, these meaningful structural variations likely play a crucial role in individual's life as they allow the transfer of more or less additional information from emitters to receivers. In line with this, the function of a vocal signal seems to influence its level of variability. Indeed, calls uttered in dangerous and urgent contexts (*e.g.* alarm and distress calls) are more stereotypic than calls uttered in more relaxed contexts (*e.g.* social affiliative calls) that display more structural variability (Bouchet, Blois-Heulin, & Lemasson, 2013; Lemasson & Hausberger, 2011; Rendall, Notman, & Owren, 2009). However, Keenan and collaborators (2013) highlighted some structural variation within alarm call's structure in male Campbell's monkeys in which males uttered very stereotypic calls in urgent alarm phases (*i.e.* beginning of a calling bout or direct visual detection of the predator) but gave more graded calls when the emergency was lower (*e.g.* end of calling bout, non-predatory events). This result not only suggests that structural variation might exist in more call types than initially suspected but also that the relationship between urgency (and implied immediate survival consequences) and acoustic stereotypy in calls is probably extremely robust and widespread. In light of this, it seems logical to find examples of acoustic flexibility in the social calls of non-human primates, and we could expect flexible call use (*i.e.* using a given call type in a particular context or with a given timing) to appear in those situations as well.

1.2.2.2.2. Flexible call use

If the acoustic flexibility of primates' vocalisation is still debated, their ability to use calls flexibly is more generally accepted (Snowdon & Hausberger, 1997). Evidence for flexible call use in primates suggest that, they possess some voluntary control on the onset of their vocalisations, the type of call given and the timing of calling.

i. Voluntary control over call emission in primates

Firstly, a line of evidence suggesting that non-human primates possess some voluntary control over their vocalisations was raised by experiments demonstrating that non-human primates can be trained to vocalize on demand (Coudé et al., 2011; Hage & Nieder, 2013; Koda, Oyakawa, Kato, & Masataka, 2007) and can also inhibit calling when an interfering noise is broadcast (Miller, Flusberg, & Hauser, 2003; Roy, Miller, Gottsch, & Wang, 2011). Interestingly, electrophysiological studies identified cortical brain areas involved during the voluntary production of calls, including areas involved in human speech production, thus confirming the role of the corticomotoneural pathway mentioned earlier in the volitional control of vocalizations in primates (Coudé et al., 2011; Hage & Nieder, 2013; Simões et al., 2010). Although this capacity was demonstrated on captive animals using operant conditioning and playback technics, it is likely relevant in the wild. Indeed, calling might firstly reveal emitter's position to 'undesirable' receivers (*i.e.* eavesdropping) and have adverse consequences. The mutism of Taï monkeys in the vicinity of a pursuit predator (*i.e.* human or chimpanzee) as opposed to the conspicuous vocal displays they produce when detecting an ambush predator (*i.e.* leopard or eagle) is a relevant example of clearly advantageous selective calling in a wild population (McGraw, 1998, pp. 133–193; Ouattara, Lemasson, & Zuberbühler, 2009a). Secondly, calling might be pointless if the background noise is too high for the call to be heard through. Here again, the vocal behaviour of Taï monkeys offers an example of the possible

importance of selective calling time as Campbell's and lesser spot-nosed monkeys give loud alarm calls in synchronized non-overlapping duets. Similarly, Schneider and collaborators (2008) showed that four sympatric species of Siberut primates all call in the morning (one quiet moment with low background noise) but that, in spite of this similar window frame, their calling bouts do not overlap.

ii. Context-dependent use of calls

Another example of flexible call use is given by studies on primate vocal interactions. For example, call exchanges in most monkey are temporally-ruled as individual respect a certain delay before responding and typically wait for the other individual to call before calling again (*i.e.* Japanese macaques: Sugiura & Masataka, 1995; common marmosets: Chow et al., 2015; Campbell's monkeys: Lemasson, Gandon, & Hausberger, 2010). Furthermore, the acquisition of correct exchange pattern seems to involve learning and progressive adjustments in young individuals (Chow et al., 2015; Lemasson et al., 2011; Lemasson et al., 2013). Male-female duets in siamangs are also temporally synchronized and the level of synchrony changes with social experience (Geissmann, 1999).

In addition, the emission of some context-specific calls seems to involve a progressive refinement during which juveniles progressively learn to use calls in the appropriate context. This was notably exemplified by the 'eagle' alarm calls of vervet monkeys (*Chlorocebus aethiops*). Juveniles firstly give this call to any flying object (including leaves) and progressively refine their calling behaviour to any bird and finally to dangerous raptors triggering aerial alarm calling in adults (Seyfarth & Cheney, 1986; Seyfarth, Cheney & Marler, 1980). In line with this, infants pygmy marmosets progressively stop using non-food calls in feeding contexts, and this seemed to be related with the frequency of food transfer and co-

occuring food calls by adults, suggesting that the behaviour may represent a form of 'coaching' by adults (Roush & Snowdon, 2001, p. 200).

Non-human primates sometimes also display flexible call use as a function of the presence, identity and reaction of social partners. Firstly, individuals are susceptible to answer more frequently to calls given by elders (Chen, Kaplan & Rogers, 2009; Lemasson, Gandon, et al., 2010; Lemasson et al., 2013) or preferred social partners (Arlet, Jubin, Masataka & Lemasson, 2015; Biben, Symmes & Masataka, 1986; Snowdon & Cleveland, 1984). Secondly, some cases of 'audience effect' have been reported in vervet monkeys, which are more likely to give alarm calls if females (*i.e.* for male callers) or juveniles (*i.e.* for female callers) are in the vicinity (Cheney & Seyfarth, 1992). Also, male blue monkeys (*Cercopithecus mitis*) give more alarm calls when a predator is close to group members than when it is further away, regardless of the distance between the male and the predator (Papworth, Böse, Barker, Schel & Zuberbühler, 2008). Finally, the emission of various call types by males (*e.g.* food calls, pan hoots) and females (*e.g.* copulation calls, greetings) can be favoured or limited by the presence, number and social status of congeners in chimpanzees (Laporte & Zuberbühler, 2010; Mitani & Nishida, 1993; Slocombe et al., 2010; Townsend, Deschner & Zuberbühler, 2008; Townsend & Zuberbuhler, 2009).

1.3. Combinatorial abilities: a possible evolutionary solution to fulfil communicative needs in spite of articulatory constrains?

The work reviewed in the previous sections highlighted that, even if non-human primates display some (limited) acoustic flexibility, it is largely exceeded by their capacity to use calls flexibly. This opens the path for a possible complexification of their repertoires via combinatorial processes.

Actually, there is a growing number of records of call combination in non-human primates and it has been proposed that combinatorial capacities allow primates to overcome their relative lack of acoustic flexibility (compared to birds or cetaceans for instance) to diversify their communication and convey complex information. This hypothesis implies that one of the key features of language might have rudimentary parallels in non-human primates. As mentioned earlier, it is difficult to make any claim on the homologous (*i.e.* inherited from a common ancestor) or analogous (*i.e.* resulting from convergent evolution) nature of combinatorial mechanisms in human and non-human primates. We propose to explore these capacities in our closest relatives with several purposes: firstly to understand the extent to which the comparison between humans and other primates can be supported in regards of call combination, secondly to shed light on the selective pressures and evolutionary mechanisms involved in the development of call combination in the primate lineage. Hence, another logical step is to define and describe precisely the vocal combinations that exist in humans and other primates.

1.3.1. Human language and combinations

Language allows humans to create a virtually infinite number of meanings from a finite number of elements (Hauser et al., 2002). This is notably possible thanks to duality of patterning (Hurford, 2008). This feature of language was initially conceptualised by Martinet (1949) and then taken by Hockett (1960) who mentions it as the thirteenth (and last) design feature of language (*i.e.* a feature present in all human languages). Duality of patterning was defined as the property of human language that enables combinatorial structure on two distinct levels: phonology and morphosyntax (de Boer, Sandler & Kirby, 2012).

i. Phonology

Phonology corresponds to the combination of meaningless sounds (*i.e.* phonemes) into meaningful elements (*i.e.* morphemes and monomorphemic words). Phonemes bear no intrinsic meaning, they are the smallest meaning-differentiating sound units in a language (Yule, 2014). To say it differently any sound which, when added or used to replace another sound in a word, changes the initial word into a new one is a phoneme. For example, in English the sounds /k/ and /b/ are phonemes as they differentiate the words "cat" and "bat". Two words that differ only by one phoneme are termed 'minimal pair'. The meaning of morphemes is not defined by any meaning attached to the phonemes composing them, consistently with the arbitrariness of languages (*e.g.* the word 'cat' has not much to do with a cat except for the social convention linking them).

ii. Morphosyntax

Morphosyntax includes both morphology, where morphemes can be combined into more complex structures (*i.e.* polymorphemic words), and syntax, where mono- and polymorphemic words are combined into sentences (Collier, Bickel, Schaik, Manser & Townsend, 2014; Tellier, 2008). Morphemes correspond to the first level of meaningful units in a language. They can be formally defined as 'a minimal unit of meaning or grammatical function' (Yule, 2014). Some words consist in only one morpheme (*i.e.* mono-morphemic words such as 'cat'). As previously mentioned, morphemes can be combined together into polymorphemic words. For example, the word "displeasing" can be split into the privative prefix "dis-", the radical (or lexeme) "pleas-" and the suffix "-ing". Both "dis-", "pleas-" and "-ing" are morphemes. But while "pleas-" can be used alone as a monomorphemic word (*i.e.* please) or in conjunction with other morphemes that will alter its meaning in different ways (*e.g.* pleasant, pleasure), the two others are never used alone but occur systematically in combination with other morphemes (*i.e.* they are bounded morphemes as opposed to free morphemes). Contrarily to phonology, the

complex structures created via morphosyntactic combinations (*i.e.* polymorphemic words and sentences) depend on the meaning (and grammatical function) of the units that constitute them and on their organisation according to grammatical rules (Hurford, 2011). These grammatical rules are the core of language generativity as this finite number of rules allows us to generate an infinite number of structures among which rules distinguishe well-formed (or grammatical) syntactic structures from ill-formed (or non-grammatical) syntactic structures (Tellier, 2008; Yule, 2014).

Most definitions of linguistic items involve (when they are not exclusively based on) an functional component. This implies that one sound can be both a phoneme, a morpheme and a word depending on the function in plays in a linguistic proposition. For example, the sound /s/ is a phoneme since it differentiates the word sinc from zink. And it is a morpheme as well since it can mark the plural form when added to another morphem as for example in the word 'cats' which is constituted by the lexical morpheme cat- and the inflexional morpheme –s. Finally "-'s" is also a word as it notably represents the contracted form of the verb "to have" in the third-person singular conjugation of simple present (*e.g.* he's got a friend).

This system of definition differs quite strikingly to most ethological definitions used to classify vocal utterances in animals (*e.g.* call type or subtype, vocal unit, call sequence…), which often imply an important structural component (Kershenbaum et al., 2014). This highlights the importance to take into account animals' cognition and notably receivers' perception and categorisation of signals when conducting studies with a comparative purpose. In the next section, we propose to review the research conducted on non-human primates' combinatorial capacities, with a special emphasis on the functional aspects of combination in primates.

1.3.2. Combinatorial abilities in non-human primates: structure and functions

We propose here to define and to review the existing examples of linguistic-like call combination described in non-human primates. The functional significance of units and their combination is a central element of the linguistic processes to which we propose to compare the results obtained in primates. Hence, we will develop here studies in which combination is associated with consistent changes in the information content of calls (and meaning to receivers when it could be verified).

1.3.2.1. Phonology-like structures

Drawing parallels with phonology in non-human primates would require: (1) a combination mechanism involving vocal units that are not associated to any particular behavioural context or emotional state, hence from which receivers could not extract information about the environment, caller's emotion or behaviour. (2) that the combination (or addition) of "meaningless" units creates a call which can be reliably associated with one/several external events or caller's internal state(s) (Engesser, Crane, Savage, Russell & Townsend, 2015).

To date, and to our knowledge, there are no examples of phoneme-like structures in primates. This is interesting to link this with the fact that, in spite of Hockett's initial assertion (Hockett, 1960), at least one human language (in its common definition of a set of socially conventional signals used by several individuals to communicate) does not possess the phonological level of articulation: the "Al-Sayyid Bedouin Sign Language" (ABSL). This language developed only recently (about 70 years ago) in a small community and lacks phonological structure (*i.e.* researchers could not identify minimal pairs of words) but possesses morphosyntactic rules (Sandler, Meir, Padden & Aronoff, 2005). This observation led authors to hypothesize that syntax and morphology might have preceded the apparition of phonology in humans as well (Collier et al., 2014). Notably, it has been argued that, morphology and syntax already allow a

significant increase in message which can possibly be conveyed, and can appear with a limited number of signals and that phonology might appear later, when the need to differentiate between a large set of signals appears as the size of signals' repertoire and population of users increases (de Boer et al., 2012). Interestingly, although we introduced phonology before morphosyntax in this manuscript, Hockett (1960) considered morphosyntax as the first layer of duality of patterning and phonology as the second.

1.3.2.2. Morphosyntactic-like structures

This layer of duality of patterning can be further split into two levels: morphology and syntax (Tellier, 2008).

i. Morphology-like combinations

A parallel capacity to morphology in non-human primates could be defined as the junction of vocal units from which receivers can extract information into a more complex structure which information content depends on: (1) the units merged together and their respective information content and (2) rules for units combination (*i.e.* systematic order of combination and eventual consistent alteration of the information conveyed by signal). Several examples of morphology-like combinations were described, both in Old World monkeys and New World monkeys.

Robinson described morphology-like call combinations in wedged-capped capuchins (*Cebus olivaceus*) (Robinson, 1984) using observational description of calls' and behavioural context of utterance, combined with structural analysis of call's acoustic features. These monkeys produce various call types that are consistently associated with distinct behavioural and/or social contexts. They also produce 9 non-random combined calls (*i.e.* which consist in the systematic combination of two distinct units) uttered in contexts intermediate between the

original contexts associated with the units composing them. The acoustic structure of the elements does not differ between simple and combined calls, however, the relevance to receivers of systematic changes in calls' structure has not been verified.

The morphology-like call combination described in cotton-top tamarins may also fit the definition we proposed (Cleveland & Snowdon, 1982). These monkeys combine a general alarm call emitted during intense disturbances (*i.e.* Type E Chirp, associated with piloerection) with a "general alerting/monitoring" call (*i.e.* Squeak) given by vigilant individuals, but not only in urgent alarm contexts. The combined calls are given in intermediate situations: when caller is still vigilant after an alarm phase but with decreased arousal (*i.e.* no piloerection visible). Here, the contexts associated with simple and combined calls as well as receivers' reaction were determined using observational data.

More recently, research studies also described combinatorial patterns in two species of Old World monkeys. Female Diana monkeys possess notably three social call types (H, L, R) associated respectively with socio-positive, neutral, and negative (*i.e.* discomfort) contexts that can be uttered alone or combined non-randomly with a fourth call type (A call) (Candiotti, Zuberbühler, & Lemasson, 2012a). The latter (A) involves an arch-shaped frequency modulation. It is uttered across a broad range of contexts but relates to caller's identity (Candiotti et al., 2012b). This fourth call type can be further split into two subtypes: Af (with a full arch) which relates very strongly to caller's identity and is uttered preferentially when visibility is low, and Ab (with a broken arch), which relates less strongly to caller's identity and is given at higher rates when visibility is good (Candiotti et al., 2012a). Observations on wild individuals confirmed that females give the six combined call types (HAf, HAb, LAf, LAb, RAf and RAb) in contexts corresponding to the contexts associated with the units that compose them.

Interestingly, the vocal repertoire of adult females in a closely related species, Campbell's monkeys, contains combined calls resembling the LA calls of female Diana monkeys: CH calls. These calls consist in low-pitched quavered structure (SH call, which resembles L calls of Diana monkeys) combined with an arched structure resembling the A calls of Diana monkeys. Here again, the arch can be full (*i.e.* CHf calls) or broken (*i.e.* CHb calls). For some reason, contrarily to Diana monkeys, female Campbell's monkeys never use the arch structure alone (*i.e.* they do not possess equivalent to "A" calls) but only use it as a 'suffix-like' item. While the socio-environmental context associated with combined calls and their components has been documented in Diana monkeys (Candiotti et al., 2012a), such information was lacking for Campbell's monkeys. This will be the topic of the fifth chapter of this manuscript.

Another morphology-like call combination was described in Campbell's monkeys. Here again, the combinatorial process involves the addition of a suffix to a call. Indeed, male Campbell's monkeys give Krak alarm calls when they detect an urgent ground danger (*i.e.* leopard predator) but give 'Hok" alarm calls when they detect an eagle predator (Ouattara, Lemasson, et al., 2009b). These calls can also be uttered in combination with an –oo vocal unit to create Krak-oo and Hok-oo combined calls which correspond respectively to a general danger of lesser urgency (*e.g.* a duiker passing by) and to an aerial danger, but less urgent than an eagle (*e.g.* a fight in an associated group of red colobus). Hence, the addition of the –oo unit seems associated with reduced urgency of dangers spotted, as suggested by observational data and predator simulation experiments (Ouattara, Lemasson, et al., 2009c).

Finally, a study reported that chimpanzees can combine most of the calls in their repertoire in combined utterances of two or more calls. Analysis of the context of emission of simple and combined structures suggested that the vocal communication of chimpanzees might involve a

morphology-like structure as combined calls were never used in contexts that differed strongly from their components (Crockford & Boesch, 2005). Depending on the type of call considered, combined calls seemed notably to be used in contexts intermediary to their components (*i.e.* pan hoots and pan grunts), to convey information about co-occurring contexts (*i.e.* pan hoots and grunts), or to combine caller's vocal signature with additional contextual information (*i.e.* pan hoots and various calls). However, many combinations described were only produced a few times and further analysis will be required to increase sample size and get a more comprehensive view of this complex system. In addition, receivers' reaction to various combination has not been assessed and authors suggested that playback experiments would be required to further clarify this question.

The examples reviewed in this section fall into two categories. The first category corresponds to the combination of calls that can also be used independently to create a structure. In this case, combination allows either a contextual refinement (*e.g.* urgent alarm 'Type E chirp' combined with the, less urgent, vigilance 'Squeak' of cotton-top tamarins creating a combined call associated with post-alarm vigilance) or the addition of information content from the two calls (*e.g.* information about contextual valence from the initial H/L or R unit and caller's identity from A calls in the combined utterances of Diana monkeys). The second category of morphology-like compounds described corresponds to the suffixation of an existing call type with a 'bounded' unit (in reference to bounded morphemes in human). Here again, the addition of an acoustic element can either modify the contextual information associated with the call (*e.g.* Hok urgent eagle alarm vs Hok-oo less urgent aerial danger) or add information to the initial call (*e.g.* female Campbell's monkeys "SH" call combined with an arch that relates more strongly to caller's identity than the initial SH unit; Lemasson & Hausberger, 2011).

ii. Syntactic-like sequences

Literature on animal sequences traditionally distinguishes two levels of organization. A first level of combination, named ‘phonological syntax’ was defined as “the concatenation of sounds without independent information content and which are not used singularly, or meaningful sounds that lose their original content when combined” (Collier et al., 2014; Hedwig, Mundry, Robbins & Boesch, 2015; Marler, 1977). The second level, ‘lexical syntax’ has been defined as the level at which meaningful elements are combined. These original definitions included the combination of call units into combined calls, which we treated in the previous sections, as well as the combination of calls into larger sequences (Marler, 1977). In the next section, we propose to review call sequences given by primates that may fit those definitions. Although we decided to use those two levels (i.e. phonological vs lexical syntax), to respect the traditional classification scheme of animal syntactic-like structures, it is important to highlight the possible cofound linked to the term ‘phonological syntax’. Indeed, this term, which does not find any equivalent in the linguistic terminology, conflates two distinct layers of articulation. This questions the relevance of this term which should be used carefully in a comparative approach with language or, eventually, replaced in future work by a more appropriate term.

Lexical syntax

Examples of sequences with a ‘lexical syntax’ were notably described in red-bellied titi monkeys (*Callicebus moloch*) which utter sequences of calls which constitution depends on the context. More precisely, they give two types of short sequences (composed of two call types): chirrup-pump and chirrup-pant sequences uttered respectively when interacting with a neighbouring group at a distance (see also Robinson, 1979b) and in situations of high arousal that often leads to caller’s withdrawing (Robinson, 1979a). In addition, they give a third

sequence: Chirrup-pant-pump sequence uttered by solitary males being chased away from a neighbouring group and during close-range encounters between groups (Robinson, 1979a). These results suggest that the context of the three-calls sequence corresponds to an intermediate between the contexts associated with chirrup-pump and chirrup-pant sequences (Caesar & Zuberbühler, 2012; Cleveland & Snowdon, 1982). In addition, a playback experiment showed that the order of call was important as subjects could discriminate between natural and reverse-order sequences (Robinson, 1979a).

Similarly, black-fronted titi monkeys (*Callicebus nigrifons*) utter long vocal sequences composed of one to three call types. These call types are associated respectively with aerial dangers (A calls), general alert including ground-related stress (B calls) and caller's intention to move (C calls) although the last call type seems less strongly associated with a given context (Cäsar, Byrne, Hoppitt, Young & Zuberbühler, 2012; Cäsar, Byrne, Young & Zuberbühler, 2012). In addition, the composition of the sequences varies with the nature of danger. For instance, pure A call sequences are given to aerial predator while mixed sequence of A, B and sometimes C calls are triggered by capuchin monkeys that black-fronted titi monkeys avoid by descending in lower strata (Caesar & Zuberbühler, 2012; Cäsar, Byrne, Young, et al., 2012). In this last case, the order of calls was not random as sequences always started with A calls, before B calls were included and eventual C calls if there were some given (Cäsar, Byrne, Young, et al., 2012).

In line with this, male Campbell's monkey possess six main call types (Boom, Krak, Krak-oo, Hok, Hok-oo, and Wak-oo) given in sequence which composition varies consistently with the type of disturbance encountered (Ouattara, Lemasson, et al., 2009b). Notably, sequences of Krak-oo calls relate to general danger and were given to a broad range of non-urgent disturbance (Ouattara, Lemasson, et al., 2009b). The addition of Krak calls to Krak-oo sequences signals the presence of a leopard while the addition of Hok, Hok-oo and/or Wak-oo

calls to Krak-oo sequences relates to the detection of an eagle, two main predators of Campbell's monkeys. In particular, the auditory detection of the presence of a leopard (hearing leopard growls or leopard alarm calls from primate neighbours), triggered mixed sequences of Krak and Krak-oo calls while the visual detection of a leopard triggered 'pure' Krak call sequences (Ouattara, Lemasson, et al., 2009b, p. 209). Interestingly, the sequence corresponding to the general alert (*i.e.* 'Krak-oo' sequences) could be further modified during non-predatory events. Notably, 'boom' calls, which trigger group gathering and travelling when uttered alone, were added at the beginning of a Krak-oo sequence when a large branch or tree was falling down. Finally, the addition Hok-oo calls to these "tree-falling" sequences (*i.e.* Boom Krak-oo sequences) occurs during inter-group encounters with neighbours (*i.e.* Booms Hok-oos Krak-oos sequences organised in this order) (Ouattara, Lemasson, et al., 2009b). The analysis of sequences' structure revealed a non-random organisation: calls relating to the most urgent contexts (*i.e.* Krak and Hok calls) systematically appear at the beginning of the sequence. Furthermore, Boom calls are always uttered in pairs (2 boom calls, separated by eight seconds). They systematically appear as the first calls in the sequence and always relate to non-predatory events and their presence was proven to be relevant to receivers (Ouattara, Lemasson, et al., 2009b; Zuberbühler, 2002).

Phonological syntax

It is important to precise that, contrarily to 'phonology-like structures' presented above, the presence of minimal pairs of calls (*i.e.* differing only by one sound unit) is not formally included in the definition of phonological syntax (Hedwig et al., 2015). This organisation has not been clearly identified yet in primates although some studies reported mixed examples which might partly rely on this system.

White-handed gibbons (*Hylobates lar*) give long call sequences that typically start with soft 'hoo' notes followed by louder notes of different types. During duets, two group members produce song in a coordinated way and 'respond' each other. Notably, when female give 'female great call' (a relatively rigid phrase composed of several notes), the duetting male generally responds with a 'male reply' phrase (which is also stereotyped) (Clarke et al., 2006). White-handed gibbons utter duets routinely in the morning but also give long call sequences in predatory context which differed in call composition and organisation (Clarke et al., 2006). The note composition of sequences differs between those two contexts: while one type of note (*i.e.* 'learning wa' notes) are globally absent from predator-induced songs, another type of notes (*i.e.* 'sharp wow' notes, that seem associated with various disturbances) are absent from morning duets. This suggests that a 'lexical' component may be involved although additional contextual information relating to these notes (in particular 'learning wa' notes) would be required to clarify this point. In addition, striking differences between call sequences appear in song structure. Firstly, predator-induced songs start with more 'hoo' notes than morning duets (on average 100 vs 9 notes). Secondly, female-specific 'great call' appears later in predatory songs and the male answers his partner's great calls more promptly in this case than during morning duets (Clarke et al., 2006). Hence in addition to differences in the note types involved, the findings reported by Clarke and collaborators also revealed differences in sequence organisation that consistently relate to the calling context, suggesting a possible 'phonological' variation. Now further research will be needed to disambiguate the "lexical", "phonological" or mixed nature of syntactic-like structures in gibbons.

Two studies on the vocalisations of Gorillas suggested that phonological syntax might be involved in these apes (Hedwig et al., 2015). Gorillas' close calls are based on five acoustic units, that can be merged together and in given longer sequences in which unit order is flexible but non-random (Hedwig et al., 2014). In addition, some acoustic units have been the subject

of more detailed analyses. The study showed that combined calls were used in contexts that corresponded to some of their components but also differed in some aspects, notably because they were more likely to be given during vocal exchanges (Hedwig et al., 2015).These studies offer promising results but will require further research as exact changes in information content of combinatorial structures and their relevance to receivers remain to be further explored. Notably, the large number of distinct combinations, including patterns given only rarely, led authors to suggest that some combinations might not differ in their informational content.

Finally, the last example of call sequences that might reflect a syntactic-like organization to our knowledge was described by Arnold and Zuberbühler (2006, 2008, 2012) in putty-nosed monkeys (*Cercopithecus nictitans*). These animals use two distinct call types (Pyow and Hack) in sequences which structure depends on the context. Indeed, males give Pyow sequences when they detect a leopard and Hack sequences when they detect an eagle. Interestingly, they also use Pyow and Hack calls in mixed sequences that do not relate to a particular predator but trigger group movement. Here, Collier and collaborators (2014) proposed two distinct interpretations: this system could involve some kind of 'phonological syntax' in which mixed sequences correspond to a context that does not reflect the contexts associated with the calls that compose them. The other interpretation proposed relies on a slightly different approach to the way Pyow and Hack calls function. Indeed, if those calls were associated respectively with the abstract meanings 'move-on-the-ground' and 'move-in-the-air', receivers might seek the contextually relevant interpretation of these calls which might have led the 'Pyow-Hack' sequences uttered in the absence of predators to combine into a general meaning 'we move' as these animals travel at various canopy levels and sometimes on the ground (Collier et al., 2014). Although this mechanism is less likely, as carefully addressed by the authors, further

investigation of the possible mental representations triggered by conspecific calls in non-human primates would be required before ruling out this interpretation.

The findings highlighted in this section revealed the existence of combinatorial capacities, possibly involving morphosyntactic-like processes relevant to receivers in various and sometimes phylogenetically distinct species of primates, including New World monkeys and Old World monkeys, as well as Asian and African apes. The parallels that can be drawn with human language remain uncertain, and further research, including experimental verification using playback experiments, will be required to understand more in depth the mechanisms involved. However, the apparent large spread of these abilities in the primate lineage is consistent with the hypothesis suggesting that combinatorial capacities might have evolved in primates to diversify their communicative repertoires and to fulfil their communicative needs in spite of articulatory constraints. Now, the question remains to assess the extent to which these combinatorial abilities actually enlarge species' vocal repertoire and allow the diversification of functionally adaptive signals. Hence, we propose to dedicate the next section to a brief review of the functions of vocal communication in primates, and more particularly of the functions of combined vocal utterances.

1.3.1. The functions and informational content of combinatorial signals

As in many animal species, vocal communication serves important functions in various aspects of non-human primates' life. It notably plays an important role in mate attraction (Delgado, 2006; Mitani, 1985), territorial defence (Bremond, 1968; Catchpole, Slater & Song, 1995; Hagen & Hammerstein, 2009; Penteriani, 2002), inter-group or inter-individual spacing (in the

case of solitary species) (Marler & Mitani, 1988; Mitani, 1985; Robinson, 1979b) or protection against predators (Caro, 2005; Macedonia & Evans, 1993; Zuberbühler, 2009).

Those functions often involve 'loud' calls which propagate over long distances (Delgado, 2006; McGregor, 1993; Wich & Nunn, 2002), but vocal communication also plays an important role in communication over short distance and 'soft' calls can function to regulate social relationships in affiliative as well as in agonistic contexts (Cheney, Seyfarth & Palombit, 1996; Cheney, Seyfarth & Silk, 1995; Kondo & Watanabe, 2009). For instance, such calls can be used to mediate dominance relationship (Kitchen, Seyfarth, Fischer & Cheney, 2003; Neumann, Assahad, Hammerschmidt, Perwitasari-Farajallah & Engelhardt, 2010), to synchronize within group activities (Radford & Ridley, 2008; Townsend, Zöttl & Manser, 2011; Uster & Zuberbühler, 2001), to signal caller's identity (Miller & Hauser, 2003; Price, Arnold, Zuberbühler & Semple, 2009; Rendall, Rodman & Emond, 1996), or membership to a social unit (Crockford et al., 2004; Tanaka et al., 2006), and to maintain group's spatial cohesion (Palombit, 1992; Poole, Payne, Langbauer Jr & Moss, 1988; Radford & Ridley, 2008). Importantly, these latter functions might be even more salient in primates than in other species due to the strongly bonded nature of non-human primates groups (Lehmann, Korstjens & Dunbar, 2007; Shultz & Dunbar, 2007).

The previous section reviewed combinatorial structures involved in both long-distance (*i.e.* "loud" calls) and short-distance communication that played important roles in several of the abovementioned functions of communication. Indeed, combinatorial structures were found in calls uttered in alarm contexts with various levels of emergency, as for instance, the proto-lexical syntax of black-fronted titi monkeys (*i.e.* A, B and C call sequences) or the suffixation-like system of male Campbell's monkey (*e.g.* Krak/Krak-oo calls; Cäsar, Byrne, Hoppitt, et al., 2012; Ouattara, Lemasson, et al., 2009c). Complex vocal utterance were also involved in territorial defence and management of inter-group encounters, as for instance the 'neighbour'

call sequences of male Campbell's monkeys and the chirrup-pan-pump sequences of red-bellied titi monkeys (Ouattara, Lemasson, et al., 2009b; Robinson, 1979b). Finally, several examples of combination, in particular for morphology-like mechanisms, concerned contact calls uttered in non-urgent social context (*e.g.* combined call of females in guenons, combined calls of wedged-capped capuchins: Candiotti et al., 2012a; Lemasson et al., 2005; Robinson, 1984).

Interestingly, some species appear to 'cumulate' several combinatorial processes through their repertoire. The most striking example is that of Campbell's monkeys in which males display both morphology-like call combination (*i.e.* suffixation) and call sequences with a 'lexical syntax'. In depth analyses of the communicative system of these animals would thus be important to provide insights into the evolutionary mechanisms leading to the joint selection of two distinct, yet complementary, combinatorial processes. Interestingly female Campbell's monkeys also give combined calls (*i.e.* CH calls) which play an important function in group social cohesion (Lemasson et al., 2003, 2005) as opposed to males' alarm calls.

This functional diversity of sound combinations in non-human primates suggests that several distinct evolutionary pressures might be involved in the development of such capacities. We propose to review shortly the main selective pressures that may influence the evolution of animals' communication.

1.4. Selective pressures influencing the evolution of communication signals

Three main selective pressures have been highlighted for their influence on animal's vocal signals: habitat, predation and social life.

1.4.1. Habitat

A species habitat is susceptible to influence at least two aspects of its communication. Firstly, the structure of the habitat, notably when it affects visibility, has been proposed as a factor influencing the sensory modality of communication. Indeed, animals living in visually dense habitats such as in the canopy of dense tropical forests, often use preferentially acoustic over visual signals (Marler, 1967). Secondly, some physical characteristics of the habitat might have influenced the structure of vocal signals (Marler, 1967). For example, dense vegetation may induce constraints by degrading and attenuating signals during sound propagation (Brown & Waser, 1988; Marten & Marler, 1977; Waser & Brown, 1986). In line with this, Cleveland and Snowdon (1982) showed that the structure of cotton-top tamarins' calls varied with the distance from which calls were generally uttered. For example, calls given in resting context (*i.e.* mostly in phase of high group cohesion), had lower frequencies and amplitudes than calls uttered by isolated individuals or during solitary exploration (Cleveland & Snowdon, 1982). More generally, species living in a dense habitat or in a noisy environment are susceptible to have evolved more robust, stereotypic and discrete signals than species living in less constraining habitat as the latter might be able to rely on multimodal communication canals to disambiguate signals (Marler 1975).

1.4.2. Predation

Predation has also been thought of as an important selective force driving the evolution of communication signals. Here again two main types of 'consequences' can be highlighted. Firstly, predation might have led to the diversification of alarm signals. Indeed, some species display a unique escape response to all their predators and may need to encode the level of emergency in their alarm calls (*i.e.* urgency-based systems). In parallel, other animals present distinct escape responses (*e.g.* being silent or mobbing the threat, escaping as a group or singly,

running in distinct directions) depending on the predator and its hunting technic (Furrer & Manser, 2009; Macedonia & Evans, 1993). In these species, the ability to signal the nature of danger (*e.g.* using predator-specific alarm calls) allows receivers to adopt the most adaptive behavioural response. Such systems, sometimes called 'referential systems', are frequently encountered in primates (Fichtel & Kappeler, 2002).

In addition, predation might have also influenced the structure of calls and calling behaviour in non-predatory contexts. Indeed, signals with various functions (alarm calls, but also begging calls and mate-attraction calls) seem to have evolved to limit detection or localization by predator in a broad range of taxa, either because of their acoustic structure (*i.e.* acoustic crypsis) or because of their limited use when a predator is in the vicinity (*i.e.* hiding) (Tungara frog: Ryan, Tuttle & Rand, 1982; Passeriformes: Briskie, Martin & Martin, 1999; Marler, 1955; Wood, Sanderson & Evans, 2000; porpoise: Morisaka & Connor, 2007; review by Ruxton, 2009).

1.4.3. Social life

A third factor susceptible to influence the evolution of communication is animals' social life. The theory proposes that increased social complexity, and the inherent need to regulate social interactions between group-members, co-evolved with increased communicative complexity. Complex social systems were defined by Freeberg, Dunbar and Ord, (2012) as "those in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time". Hence, various factors might influence social complexity, such as group size, the number of distinct social roles in a group, the diversity of interactions an individual can have with others as well as their frequency. In parallel Freeberg and collaborators (2012) defined complex communicative systems as 'those that contain a large number of structurally and functionally distinct elements (*e.g.* large

display repertoire sizes) or possess a high amount of bits of information". This definition implies that complex communication can be reflected both in the diversity of signals and in the variability within a type of signal (*e.g.* more or less variable acoustic structure of a given call type).

The study of the co-evolution between social and communicative complexity has been the topic of extensive theoretical interest. Several studies also tested this hypothesis empirically, notably by comparing the communication of species with distinct social systems (*i.e.* marmots: Blumstein, 2003; mongooses and meerkats: Manser et al., 2014; whales: May-Collado, Agnarsson & Wartzok, 2007, primates: Gustison, Roux & Bergman, 2012; McComb & Semple, 2005). Such studies highlighted a relationship between social complexity and signal diversity as for instance they reported a positive correlation between repertoire size and complexity of mating systems (Kroodsma, 1977), between the number of alarm calls and diversity of social roles (Blumstein, 2003) and between the complexity of social structures and repertoire diversity and size (Manser et al., 2014), including number of combinatorial patterns (Bouchet et al., 2013).

Furthermore, as highlighted by Freeberg (2012), social complexity is also susceptible to influence use and variability within a signal category. Notably, Manser and collaborators (2014) highlighted that mongoose species with a more complex social life had more graded vocal repertoires, presented calls with a higher potential to signal identity that were meaningful to receivers in some social contexts (Reber, Townsend & Manser, 2013; Townsend et al., 2011) and used calls more flexibly, notably in combination (Jansen et al., 2012; Manser et al., 2014).

Hence, both habitat, predation and social life seem to influence the structure and sometimes the use of acoustic signals in animals. If combinatorial abilities occurred as an evolutionary solution to overcome the limited capacities of call production displayed by non-human

primates, we may be able to identify traces of the same selective pressures in the combinatorial systems of primates.

1.5. Objectives of the thesis

There is an increased interest in the combinatorial abilities present in the vocal communication of animals, notably because their characterization might help us to get insights into possible mechanisms that drove the development of the complex organisation of language. Non-human primates are frequently used as models for such studies as they often display neuro-anatomical and socio-ecological characteristics that place them as good candidates to develop combinatorial vocal structures. However, we know so far relatively little about the structural properties, functions and possible evolutionary paths of the combinatorial systems described and we propose to contribute to the development of this research area. In particular, this thesis proposes to bring additional information about morphology-like structures in primates. Using both experimental tests and observational data, this thesis aims to characterise more precisely the possible proto-morphological structures present in the communication of two species of guenon, their relevance to receivers and to propose hypotheses about their possible functions and evolution.

1.5.1. Relevance of our biological models

This thesis focused on two species of arboreal cercopithecids: Campbell's monkey and Diana monkeys. These two species diverged about 3.5 million years ago (Tosi, Detwiler & Disotell, 2005), and live sympatrically in the primary forests of West Africa (Kingdon, 2015). Extensive descriptions of Campbell's and Diana monkeys' ecology, habitat, social life and vocal repertoires are provided in Chapters 2 and 6 of this thesis. They constitute remarkable models

for the study of vocal communication, notably in regards of its combinatorial properties for several reasons. Firstly, their visually dense habitat makes difficult visual communication and these animals communicate essentially through the auditory sensory modality in both alarm and affiliative contexts and at both intra- and inter-group levels (Candiotti et al., 2012a; Lemasson & Hausberger, 2011; Ouattara, Lemasson, et al., 2009b; Zuberbühler, Noë & Seyfarth, 1997). They hence display relatively discrete vocal repertoires with easily identifiable call types and subtypes (Candiotti et al., 2012a; Lemasson & Hausberger, 2011; Zuberbühler et al., 1997). Secondly, these animals are preyed-upon by distinct predators with varied hunting technics (*i.e.* ambush and pursuit) and, as a likely consequence, developed referential alarm calls in both males and females sex-specific repertoires (Ouattara, Lemasson, et al., 2009a, 2009b; Zuberbühler, 2000b; Zuberbühler et al., 1997), as well as differentiated behavioural responses to their various predators (Ouattara, Lemasson, et al., 2009a; Zuberbühler, 2007). Importantly, groups of the two species tend to associate on a regular basis and cooperate in anti-predatory response, notably thanks to interspecific communication as they respond to each other's alarm calls with their own (functionally congruent) alarm calls (Zuberbühler, 2000a). Thirdly, Campbell's and Diana monkeys live in female-bonded harem groups and display a rich social life and complex social communication (Candiotti et al., 2015). Socially-guided acoustic plasticity, temporally-ruled call exchanges, arousal state and individual identity acoustic coding were found in both species' female contact calls (Candiotti et al., 2012a, 2012b; Lemasson et al., 2011; Lemasson & Hausberger, 2011; Lemasson & Hausberger, 2004; Lemasson et al., 2012). Lastly, the vocal repertoire of males and females in both species involve various types of combinatorial structures, as mentioned earlier, but the extent to which call combination occurs differs, offering here a remarkable chance to conduct comparative studies.

1.5.2. Focus on some morphology-like combinatorial patterns in our study species

Male loud alarm calling in Campbell's monkeys

As explained above, male Campbell's monkeys produce two predator-specific alarm calls, *i.e.* Krak (for leopard) and Hok (for eagle), as well as other more general alarm calls (for less urgent dangers), among which Krak-oo and Hok-oo calls. Experimental studies demonstrated earlier the referential value of both Krak and Hok calls for Campbell's monkeys, as well as the ability of sympatric Diana monkeys to 'decode' the predator meaning (Zuberbühler, 2000a, 2001). Observational studies suggested that Krak-oo and Hok-oo calls possibly result from a suffixation mechanism involving the addition of an 'oo' unit after Krak and Hok stems, aiming to attenuate the degree of threat signaled. However, experimental procedures testing the combinatorial nature of this possible suffixation mechanism and its relevance to receiver were still lacking.

Female contact calling in Campbell's and Diana monkeys

The vocal repertoires of females in both species mostly rely on contact calls. Each species possesses high-pitched trills, low-pitched quavers, and arched frequency-modulated calls which seem to function mostly to maintain group socio-spatial cohesion (Candiotti et al., 2012b; Lemasson et al., 2003, 2005; Uster & Zuberbühler, 2001). In both species, the arch counts two subtypes, a complete arch and an arch with truncated top (*i.e.* broken arch). Acoustic analyses have shown that the quavered call and the arch respectively code for emotional state/valence and individual/social identity (Candiotti et al., 2012a, 2012b, Lemasson et al., 2005, 2012). Moreover, studies have described non-random patterns of combination of these different structures (Candiotti et al., 2012a; Lemasson et al., 2005). Females in both species utter combined calls consisting in the combination of the low-pitched quavered call with the arched vocal unit (both the complete and broken subtypes can occur in combination). But the

two species differ quite strongly in their use of call combination: female Campbell's monkeys only display the aforementioned combined structures and the context in which the distinct types (*i.e.* simple or combined) and subtypes (*i.e.* complete or broken arch) are given remains unclear. Diana monkeys further combine other call units of their repertoires (*i.e.* high pitched trills and repetitive 'discomfort' calls) with arched structures. An observational study suggested that the combinatorial system of female Diana monkeys might be compositional (*i.e.* based on the linear concatenation of call units into combined calls which 'meaning' depends on their components) but this hypothesis has never been tested experimentally.

1.5.3. Questions

This thesis notably follows-up several years of work investigating the vocal communication of Campbell's and Diana monkeys that highlighted important aspect of their anti-predatory, social, and interspecific communication. The studies showed that these animals possess a complex communication system involving context-specific signals and also suggested that combinatorial processes are involved in the constitution of several calls given by Campbell's and Diana monkeys. Nevertheless, if experimental validation had confirmed the referential properties of alarm calls in both species, the only work conducted on the combinatorial properties of calls in both species remained observational.

Hence, a logical first step has been to verify experimentally the combinatorial nature of male Campbell's monkeys alarm calls.

1/ Do male Campbell's monkey suffixed Krak-oo calls really consist in the linear combination of a Krak call with an -oo unit? In other words, can we recombine Krak calls into Krak-oo calls by simply adding an 'oo' unit and conversely, create recombined Krak calls by deleting the 'oo' unit of a Krak-oo call? (see Chapter 3).

Secondly, observational studies suggested that female Diana monkeys utter combined calls composed of an introductory unit, which relates to the general context, merged with an arched structure which relates to caller's identity. We tested experimentally the combinatorial nature of these vocalisations using a procedure similar to the one conducted in question 1:

2/ Do the combined calls of female Diana monkeys consist in the linear combination of two acoustic units relating respectively to contextual valence and caller's identity? In particular, does the artificial replacement of one unit in the call by another triggers predictable changes in receivers' behaviour? (see Chapter 4).

The social significance and potential to convey caller's identity of arched structures had already been demonstrated experimentally in Campbell's monkeys but, contrarily to Diana monkeys, the context associated with the emission of the various simple and combined call types and subtypes (*i.e.* with a full or broken arch) remained unclear. Hence, we proposed to study in more details the context of emission of contact calls in wild female Campbell's monkey:

3/ What contextual social and ecological variables relate to the emission of simple and combined calls (sub)types in wild Campbell's monkeys? (see Chapter 5).

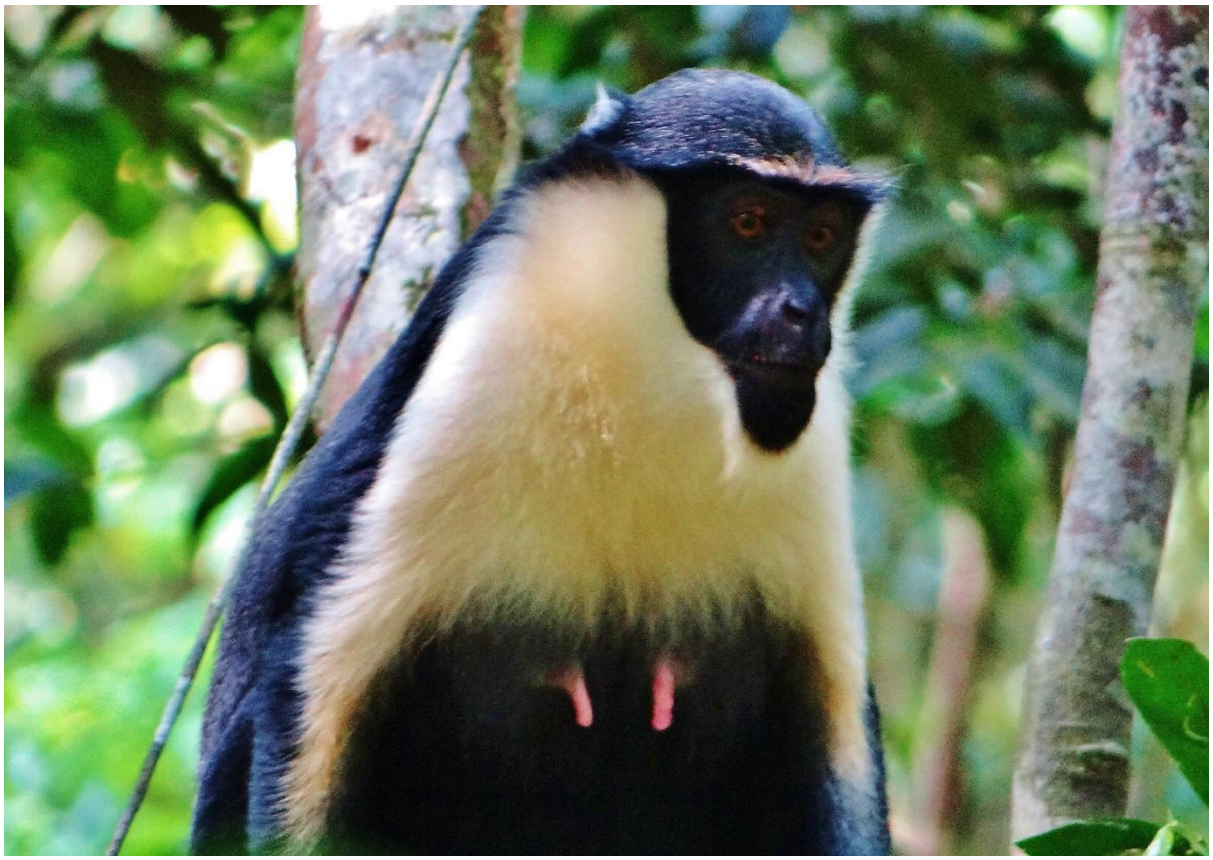
Finally, these two closely related species possess the same basic repertoire of acoustic structures and face similar ecological constrains with similar social structures (one-male multi-female groups). However, the two species also differ in several aspects: (1) they display obvious distinct strategies to face these constraints (Campbell's and Diana monkeys showing

respectively cryptic and conspicuous non-vocal behaviours); (2) they differ slightly in terms of social organization (group size and degree of bonding); (3) they vary significantly in the use of their homologous acoustic structures (call rates and types of combinations). Reviewing the detailed knowledge we possess of their communication and behaviour with the data gathered through long-term field studies, we propose to answer two questions:

4/ Does the vocal repertoire and the flexible call use of Diana and Campbell's monkeys reflect their cryptic *vs* conspicuous strategies? How may socio-ecological factors explain differences in the diversity of call combination? (see Chapter 6).

CHAPTER 2

GENERAL METHODS



GENERAL METHODS

This section describes the species, the populations and the individual subjects studied during this PhD as well as the general methodologies used. Detailed descriptions of procedures (sampling methods and experimental protocols) will be developed for each study in the corresponding chapters.

2.1. The Taï National Park

2.1.1. Geographical situation and climate

The Taï National Park (TNP) is a tropical evergreen lowland forest in the South-West part of Cote d'Ivoire, in West Africa (5° 20' – 6° 10' N; 6° 50' – 7° 25' W; Fig. 1). It is one of the largest intact segments of the Upper Guinea Forest (5364 km², TNP official survey). It has a tropical rainy climate, with stable temperatures over the year (average 24°C, McGraw, 1996) and alternation of dry seasons (December – February and July – August) and wet seasons (March – June and September – November) with an average annual rainfall of 1942mm (Korstjens, 2001). Vegetation mainly consists of a dense ombrophilous forest with a continuous 40 to 60 meters canopy and emergent trees (Riezebos, Vooren, & Guillaumet, 1994).

Figure 1: Location of the Taï National Park, Cote d'Ivoire. Picture credits africannaturalheritage.org.

2.1.2. Study site

Our research was conducted within the area located in the western part of the Taï National Park, near the CRE (Centre de recherche en écologie) research station (5° 50' N, 7° 21' W) under the supervision of the 'Taï Monkey Project'. This project was initially funded by Ronald Noë in 1991 and is now under the direction of Klaus Zuberbühler and Scott McGraw. It is managed in collaboration with the 'Centre Suisse de Recherche Scientific' in Abidjan and maintains a camp in the park (Fig. 2), a grid of trails in the research area as well as a continuous survey of habituated monkey groups within the area by local field assistants.

Figure 2: Research camp of the Taï monkey forest.

2.2. Fauna

2.2.1. Non primate fauna

The Taï National Park hosts a remarkably diverse fauna including 128 species of non-primate mammals, counting notably two felids (leopards and African golden cat *Profelis aurata*), Western tree hyraxes (*Dendreohyrax dorsalis*) and four ungulate species endemic of the Upper Guinea forest: pigmy hippopotamus (*Hexaprotodon liberiensis*), Zebra duiker (*Cephalophus* zebra), Ogilby's duiker (*C. ogilbyi*) and Jentkin's Duiker (*C. jentnki*) (Hoppe-Dominik, 1995; Riezebos et al., 1994). The avifauna counts more than 200 bird species including black-casqued hornbills (*Ceratogymna atrata*) which discriminate between Diana and Campbell's monkeys respective 'leopard' and 'eagle' alarm calls (Rainey, Zuberbuhler, & Slater, 2004). Forty-two species of reptile live in the park, including crocodiles (*e.g.* Nile crocodile *Crocodylus*

niloticus), a species of turtle (African softshell turtle *Trionyx triunguis*) as well as various species of snakes including Gaboon adder (*Bitis gabonica*) and Royal Python (*Python regius*) (Riezebos et al., 1994). More than 250 insect species were identified, which likely represent only a small part of the whole but yet unidentified entomological fauna of this area (Allport, Boesch, Esser, Merz, & Piart, 1994).

2.2.2. Predators of our study species

The Taï National Park counts 4 large-bodied predators (one bird and three mammals) which regularly prey on the Taï monkeys: crowned hawk-eagles, leopards, chimpanzees and human poachers.

Crowned hawk-eagles (*Stephanoaetus coronatus*) are large diurnal birds of prey weighting 2.5 to 4.7 kg (Del, Elliot, & Sargatal, 1994) which feed primarily on monkeys and duikers. They are ambush predators and mostly adopt a sit-and-wait strategy, hiding in a tree in front of an approaching group and waiting for a prey to be underneath their perch to attack (Shultz & Thomsett, 2007). When detecting an eagle, monkeys often engage in loud alarm calling, which often leads the eagle to give up and leave.

Leopards (*Panthera pardus*) are the largest felids in Taï. They show both diurnal and nocturnal activity phases and have a large prey spectrum (Jenny & Zuberbühler, 2005). They are ambush predators hiding and approaching slowly their prey before making a kill. Similarly to eagle, the discovery of a leopard by a group of monkeys triggers extensive and loud alarm calling after which the leopard tends to give up its hiding position and move on (Zuberbühler & Jenny, 2002). Interestingly, a radio-collar follow of leopards in Taï showed that they likely develop individual preferences for a few prey species (Zuberbühler & Jenny, 2002).

Groups of chimpanzees (*Pan troglodytes verus*) in Taï hunt preferentially on two monkey species: red colobus (*Colobus badius*) and black-and-white colobus (*Colobus polykomos*). The hunting pattern of chimpanzees varies seasonally, with a peak between August and October, during the period of low food availability (Boesch & Boesch, 1989; Stanford, Wallis, Matama, & Goodall, 1994). Chimpanzees hunt cooperatively in a coordinated fashion involving different roles (*i.e.* chasing the monkeys out of their hiding trees, blocking the escape routes). They actively seek for groups of monkeys and, contrarily to crowned eagles and leopards, they do not abandon their prey but start screaming after being detected (Bshary, 2007). When detecting chimpanzees, all the monkeys in Taï tend to adopt a cryptic strategy and either move silently in the opposite direction or hide in dense foliage and remain silent (Mcgraw & Zuberbühler, 2008).

Although the research area is fairly well protected from poaching, human poachers continue to hunt regularly on monkeys in other parts of the Taï National Park (McGraw, Zuberbühler, & Noë, 2007, pp. 290–310). As chimpanzees, human are pursuit hunters able to follow and reach mobile monkeys in the canopy and, as a likely result, monkeys adopt a cryptic behaviour when detecting humans as well (Kone & Refisch, 2007). Poachers often imitate animal calls (leopard and eagle calls) to trigger alarm calling and locate groups close-by. Interestingly, monkeys living in areas with high poaching pressure are not fooled by human imitations and remain cryptic when hearing them (Bshary, 2001).

2.3. Primates of the Taï National Park

Twelve species of primate have been identified in the park (Chatelain, Kadjo, Kone, & Refisch, 2001). There are three prosimian species *i.e.* Bosman' Potto, (*Perodicticus potto*), Dwarf galago (*Galago demidovii*) and Thomas's Bushbaby (*Galago thomasi*). Western chimpanzee (*Pan troglodytes verus*) as the only ape species but the park further count eight species of

monkeys, given here in growing order of body size: Campbell's monkeys (*Cercopithecus Campbelli*), lesser spot-nosed monkeys (*C. Petaurista*), Diana monkeys (*C. diana*), putty-nosed monkeys (*C. nictitans*), olive colobus (*Procolobus verus*), sooty mangabeys (*Cercocebus atys atys*), red colobus (*P. badius*) and black-and-white colobus (*Colobus polykomos*).

2.3.1. General presentation

The monkeys of Taï display various distinct social systems: the four guenon species live in harem group composed of one male and several adult females (*C. campbelli*: 3-7, *C. diana*: 6-10, *C. nictitans*: 2-4, *C. petaurista*: 4-9) (Arnold & Zuberbühler, 2006; Buzzard & Eckardt, 2007). Sooty mangabeys, red and black and white colobus live in multi-male multi-female groups of respectively 69.7, 52.9 and 15.4 individuals on average (Buzzard & Eckardt, 2007, p. 298; Korstjens, 2001). Finally, group composition for olive colobus is more variable but they are typically found in groups of several (1-3) adult males and two or more adult females (Korstjens, 2001; McGraw, 1998, p. 15).

Except for putty-nosed monkeys, which occur only at low densities in the northern region of the park, all the other species are commonly found throughout the area, at densities above 10 individuals per km² (McGraw et al., 2007). This population has been the under focus of research on various aspects of their lives (feeding ecology, anti-predator behaviour, vocal communication, social life…McGraw et al., 2007) and groups habituated to the presence of human observer have been followed on a regular basis for more than twenty years (about two groups per species).

2.3.2. Phylogeny

All the monkeys in Taï belong to the *Cercopithecidae* family and *Cercopithecinae* subfamily. The four guenons (*i.e. C. petaurista*, *C. nictitans*, *C. diana* and *C. campbelli*) are cercopithecini, sooty mangabeys are the only papionins in Taï while olive, red and black and white colobus belong to the colobini tribe (Perelman et al., 2011) (Fig. 3).

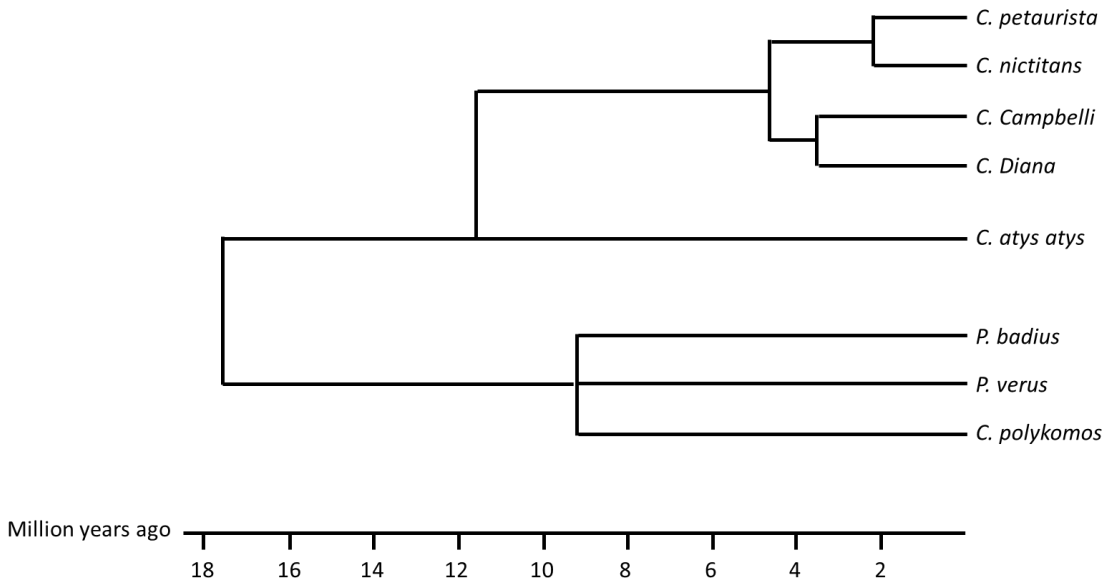


Figure 3: Estimated dates of divergence between the eight monkey species of the Taï forest (McGraw, 1998, p. 10; Perelman et al., 2011; Tosi, Detwiler, & Disotell, 2005).

Lesser spot-nosed and putty-nosed monkeys diverged most recently (2.2 million years ago, from now MYA), while Diana and Campbell's monkeys diverged about 3.5 MYA (Tosi et al., 2005) (Fig. 3). Divergence between the three colobine species occurred about 9.2 MYA, the divergence date between colobini and papionini was estimated 17.57 MYA and the divergence between papionini and cercopithecini 11.5 MYA (Perelman et al., 2011).

Diana monkeys belong to the Diana superspecies, which regroups 2 subspecies: *C. diana roloway* and *C. diana diana* living respectively on the east and west side of the Sassandra river (Oates, 1988). Campbell's monkeys belong to the Mona superspecies which regroups 4 species: *C. mona*, *C. pogonias*, *C. wolwi* and *C. campbelli* (Booth, 1955). The Diana superspecies is the closest monophyletic group to the Mona superspecies (Grubb et al., 2003;

Oates, 1988). *C. campbelli* can further be splitted in two subspecies: *C. cambpelli campbelli* and *C. campbelli lowei* which also live respectively on the east and west sides of the Sassadra river (Oates, 1988). Hence, the Taï forests hosts the *C. diana diana* and *C. campbelli campbelli* subspecies only.

2.4. Study species: Campbell's and Diana monkeys

2.4.1. Campbell's monkeys

Campbell's monkeys are the smallest monkeys of the Taï community, they have a cryptic physical aspect with olive-grey coat, white chest and neck, dark brown limbs (Fig. 4) and they tend to adopt a cryptic behaviour as well (McGraw et al., 2007, p. 25; Ouattara, 2009). Campbell's monkeys live in harem group of 9.3 individuals on average with one adult male, 3 to 7 adult females and their offspring (Buzzard & Eckardt, 2007; Ouattara, 2009; Ouattara, Lemasson, & Zuberbühler, 2009a). Home range size averages 56 ha and groups actively defend their territory against intruders (Buzzard & Eckardt, 2007; Ouattara, Lemasson, & Zuberbühler, 2009b). There is a strong sexual dimorphism in adults, with mean body weight of 4.5kg for males and 2.7kg for females (Oates et al., 1990) and juveniles reach maturity at about 3 years of age (Lemasson & Hausberger, 2011). Campbell's monkeys adapt to various habitats and live in both primary and secondary forests (Bi et al., 2008) as well as in peri-urban forest patches (Pers. obs). They count among the most common primate species of Western Africa (McGraw, 1998) and are listed as *Least concern* on the IUCN red list (Oates, Gippoliti, & Groves, 2008a).

2.4.2. Diana monkeys

Diana monkeys are brightly coloured and conspicuous monkeys, with black and auburn coats, black limbs with a white stripe on the legs, a white chest and red hairs on the rump (Fig. 4). Diana monkeys live in harem group of 23.5 individuals on average, with one adult male, 9 to 13 adult females (mean 11.5) and their offspring. Home range size is 56.8ha on average and groups defend actively their territory (Buzzard & Eckardt, 2007; McGraw, Plavcan, & Adachi-Kanazawa, 2002). As Campbell's monkeys, individuals reach sexual maturity at about 3 years of age (Byrne, Conning, & Young, 1983) and a marked sexual dimorphisms distinguishes males (5.2kg on average) from females (3.9kg on average) (Buzzard & Eckardt, 2007; Oates et al., 1990). These monkeys live only in undisturbed primary forests (Oates, 1988; Whitesides, 1989), their population is decreasing due to habitat loss and hunting and they are listed as *Vulnerable* on the IUCN red list (Oates,Gippoliti, & Groves, 2008b).

Figure 4: Pictures of wild (a) Campbell's and (b) Diana monkey of the Taï National Park, Ivory Coast.

2.4.3. Vocal repertoires of Campbell's and Diana monkeys

We only provide here a brief summary of males' and females' vocal repertoires in both species as they are developed further throughout the thesis.

Males vocal repertoires

The males of both species utter almost exclusively loud calls, in alarm or territorial contexts (Candiotti et al., 2015). Male Diana monkeys give three acoustically distinct call types repeated in long call bouts to leopards, eagles and general disturbances such as large branches falling (Zuberbühler, 2000b; Zuberbühler, Noë, & Seyfarth, 1997). A playback study further confirmed their referential nature as the type of call uttered varied consistently with the type of stimulus (mimicking either the presence of a leopard or of an eagle via broadcast of these predators' vocalisation) but not with the distance (*i.e.* close *vs* far) nor location (*i.e.* on the ground or in a tree) of the speaker relative to the group (Zuberbühler, 2000b). Male Campbell's monkeys use regularly six distinct call types (*i.e.* Boom, Krak, Krak-oo, Hok, Hok-oo and Wak-oo) (Keenan, Lemasson, & Zuberbühler, 2013; Ouattara, Lemasson, et al., 2009b) that can be combined in complex sequences which structure and composition depend on the type of event encounter. A series of playback experiments further confirmed the relevance of sequence composition to receivers (Zuberbühler, 2000a, 2002). In addition, observational studies suggested that Krak-oo and Hok-oo calls, given in less urgent situations, result from a suffixation mechanism involving the addition of an 'oo' unit after Krak and Hok stems, which are associated with more urgent threats (*e.g.* mainly leopards and eagles respectively).

Females vocal repertoires

As opposed to adult males, adult females share their vocal repertoires with juveniles (*i.e.* under 3 years old). Females of both species utter predator-specific alarm calls to leopards and

crowned-hawk eagles as well as general alert and discomfort calls when spotting a less urgent danger (Candiotti, Zuberbühler, & Lemasson, 2012a; Ouattara, Lemasson, et al., 2009a; Zuberbühler et al., 1997). However, their repertoires mostly rely on contact calls : adult female Campbell's and Diana monkeys possess each a social threat call, high-pitched trills given in socio-positive contexts, low-pitched quavers, and arched contact calls that seem to function mostly to maintain group cohesion (see pp 169-170 and p173 for sonograms and schematic representation of females' vocal repertoires) (Candiotti, Zuberbühler, & Lemasson, 2012b; Lemasson, Gautier, & Hausberger, 2003; Lemasson, Hausberger, & Zuberbühler, 2005; Uster & Zuberbühler, 2001). The arched call counts two distinct subtypes, including either a complete arch or an arch with truncated top (*i.e.* broken arche). Females in both species utter combined calls consisting in the combination of a low-pitched quavered call with an arched vocal unit (both the complete and broken subtypes can occur in combination). But the two species differ quite strongly in their use of call combination: female Campbell's monkeys only display the aforementioned combined structures and the context in which the distinct types (*i.e.* simple or combined) and subtypes (*i.e.* complete or broken arch) are given remains unclear. Diana monkeys further combine other call units of their repertoires (*i.e.* high pitched trills and repetitive 'discomfort' calls) with arched structures.

2.5. Polyspecific associations of monkeys in the Taï National Park

2.5.1. Patterns of association

One of the most striking particularity of Taï monkeys is their habit to form polyspecific associations on a regular basis (Galat & Galat-Luong, 1985). Very often, groups of several species share the same territory, actively seek for each other and spend more than 50% and sometimes up to 85% of their time in association (Mcgraw & Zuberbühler, 2008; McGraw et al., 2007, pp. 317–318). Importantly, the association between groups is not limited to spatial

aggregation but also involves heterospecific interactions, both positive (grooming, juvenile chase play, contact call exchange) and agonistic (individuals threatening, supplanting or stealing food from others). The various species display preferential association partners, and distinct roles in this "supra-specific" social organisation (Gautier & Gautier-Hion, 1983; McGraw et al., 2007). Diana monkeys are a 'central' species, they have a 'dominant' position over the other guenons in the community (*i.e.* Campbell's, lesser spot-nosed and putty-nosed monkeys) (Buzzard, 2006a; Eckardt & Zuberbühler, 2004; Oates et al., 1990) and several species (of guenons and colobus) actively maintain association with them (Mcgraw & Zuberbühler, 2008; Oates & Whitesides, 1990; Wolters & Zuberbühler, 2003).

Monkey groups cohabit and heterospecific individuals can sometimes be observed in close physical proximity although generally the monkeys of Taï use distinct strata (Galat & Galat-Luong, 1985) (Korstjens, 2001). McGraw (2007) determined four profiles of strata use in Taï: "High canopy dwellers" (*i.e.* mostly using the main canopy and emergent layer, 25 – 40 meters), "canopy generalists" (*i.e.* using a broad range of levels from lower strata to the emergent layer), "understory specialists" (*i.e.* spending most of their time under 25 meters high and rarely using the highest strata) and ground dwellers (*i.e.* spending most of the time on the ground). While red and black and white colobus were classified as high canopy dwellers, olive colobus was classified as understory specialist, using mostly stratum 2 (*i.e.* 5 to 15 meters). The four guenon species can be grouped in two distinct pairs that differ in their strata use: Diana and putty-nosed monkeys are canopy generalists, using every layer in spite of a marked preference for strata 2 (5-15 m) and 3 (15-40 m) (Eckardt & Zuberbühler, 2004). In parallel, Campbell's and lesser spot-nosed monkeys are clear understory specialists, rarely climbing above 25 m and using mainly ground and low stratum. Finally, sooty mangabeys are apart from their arboreal 'neighbours' as they were classified as ground dwellers, spending most of their time on the ground and rarely using the highest canopy strata (McGraw, 2007).

2.5.2. Potential benefits and costs of polyspecific association

Benefits

Although joint defence of a shared territory may be an advantage of heterospecific association, some authors suggested that an important advantage of living in polyspecific group lies in protection against predators (Mcgraw & Zuberbühler, 2008; Wolters & Zuberbühler, 2003). Increased protection results firstly, "mechanically", from increased density of individuals in the area, with a mechanism similar to the one observed in any gregarious group (Mcgraw & Zuberbühler, 2008). Indeed, bigger groups are generally associated with dilution effect (*i.e.* reduced per capita risk of capture), improved predator detection and decreased individual vigilance time (Sterck, Watts, & Schaik, 1997; van Schaik, 1983).

Moreover, the cooperation between individuals from different species provides additional benefits. Firstly, males of various species cooperate to chase and attack eagles, and red colobus and putty-nosed monkeys seem to be very valuable association partners in this regard (Bshary & Noë, 1997; Eckardt & Zuberbühler, 2004). On the opposite side, the presence of sooty mangabeys decreases strongly ground predator pressure and triggers a broader use of low strata by arboreal species using mostly upper-canopy the rest of the time (McGraw & Bshary, 2002). Finally, Diana monkeys detect predators approaching from the ground (including chimpanzees) before the other species and from longer distances (Noë & Bshary, 1997). Several species (*i.e.* olive and red colobus, Campbell's and lesser spot-nosed monkeys) actively seek and maintain association with Diana monkeys, notably when hearing chimpanzee calls (Bshary, 2007) and authors identified increased protection against predators as the main factor leading this behaviour (Bshary, 2007; Buzzard, 2006b).

Costs

Nevertheless, if polyspecific association undoubtedly provides increased safety, it also has down-sides. The most striking is once again a "mechanical" consequence of increased density of individuals with close ecological niches living in the same area: increased competition to access the most valuable feeding resources (Sterck et al., 1997; van Schaik, 1983). Interspecific feeding competition seems to apply mostly between species from the same subfamily, with close ecological niches (*i.e.* between the four guenon species on the one hand and between the two 'large' colobus species, namely red colobus and black and white colobus) (Buzzard, 2006b; Eckardt & Zuberbühler, 2004; Korstjens, 2001). The most striking example of this trade-off between anti-predator benefits and feeding competition was described by Eckardt & Zuberbühler, (2004) on the association between Diana and putty-nosed monkeys. They occupy very similar ecological niches and Diana monkeys associated with putty-nosed monkeys when fruit availability was high but aggressively harassed and chased them as fruit availability decreased, leading to a significant drop in association rate during these months (Eckardt & Zuberbühler, 2004). Interestingly, while diet overlap led to intolerance and avoidance between groups of Diana and putty-nosed monkeys, it led to increased dietary divergence between Campbell's and Diana monkeys during months of food scarcity (Buzzard, 2006b). This latter phenomenon was described in other studies investigating ecological partitioning among primate communities and it likely allows sympatric species with close ecological niche to benefit from association while keeping down the costs (Galat & Galat-Luong, 1985; Gautier & Gautier-Hion, 1983).

Finally, this drawback of polyspecific association must be toned down: although feeding competition exists and plays a role in the regulation of association patterns and relationships between heterospecific individuals (Buzzard, 2006a; Eckardt & Zuberbühler, 2004), individual food intakes increases thanks to decreased vigilance time and broader strata use by

individuals. This is for instance the case of Diana and Campbell's monkeys which exploit their ecological niche more broadly when they are in association (Wolters & Zuberbühler, 2003).

2.5.3. Vocal interactions

All the primates in Taï give loud calls when facing a danger (typically a predator) (McGraw et al., 2007, p. 31). Moreover, distinct call types could be associated with precise contexts of emission in Olive colobus, black and white colobus, putty-nosed monkeys, Diana and Campbell's monkeys and further studies showed that these calls were meaningful to conspecific receivers in the last four species cited (Arnold & Zuberbühler, 2008; Bene, Ouattara, Bitty, & Inza, 2012; Ouattara, Lemasson, et al., 2009b; Ouattara, Lemasson, & Zuberbühler, 2009c; Schel, Candiotti, & Zuberbühler, 2010; Zuberbühler et al., 1997).

The cooperative anti-predatory behaviour of monkeys in polyspecific troops relies strongly on vocal interactions between heterospecific callers (Gautier & Gautier-Hion, 1983), and the interspecific communication in these troops has several remarkable characteristics. Firstly, a playback study on captive individuals showed that some cercopithecids can discriminate familiar and unfamiliar voices of heterospecific individuals (Candiotti, Zuberbühler, & Lemasson, 2013). Secondly, during predator encounters, when the males of distinct species join their calling bouts, Campbell's and lesser spot-nosed monkeys seem to coordinate their calling behaviour in synchronised sequences (termed "duets") within which calls of the two males succeed each other with no overlap (*i.e.* as if they "took turns" to call) (McGraw, 1998). Finally, playback experiments demonstrated that alarm calls of some species were also meaningful to heterospecific receivers. Campbell's and Diana monkeys have been subject to intense study in this regard (Zuberbühler, 2007). Males of the two species emit referential loud calls to various dangers (*e.g.* leopard, eagle, branch falling) and when hearing the predator-

specific alarm calls of the associated male, heterospecific receivers react as if the predator was present and respond with their own referential alarm calls (Zuberbühler, 2000a, 2002).

2.6. Data collection

2.6.1. Study groups and subjects

This thesis involved habituated groups of wild Diana and Campbell's monkeys living in the study grid near the research camp of the Taï Monkey Project and followed regularly since 1990, as well as unhabituated groups of Diana monkeys living in a 50km² area around the CRE research station. Observational data were collected regularly on habituated groups of Diana and Campbell's monkeys, while unhabituated groups were only exposed to experimental playback settings.

In total four habituated groups of Diana and Campbell's monkeys (*i.e.* Diane 1, Diane 2, Cam 1 and Cam 2), were observed regularly. They consisted of one adult male, several adult females and their offspring (Table 1). All the adult members were identified using morphological characteristics (body size, scars, nipples and tail shape). We could discriminate between sub-adults (2 to 3 years old), juveniles (1 to 2 yo) and infants (<1 yo) using body size but immature individuals could rarely be individually identified, notably in Diana monkeys, due to limited distinctive signs (Buzzard & Eckardt, 2007). Cam 1 and Diane 2 had roughly the same territory, neighbouring the territory shared by Cam 2 and Diane 1. The home ranges were of equivalent size (0.53 ha and 0.56 ha respectively) and overlapped slightly (Ouattara, Lemasson, et al., 2009b). The adult male of Cam 1 (Darius) was supplanted by a new male in December 2006 (Kili) (Ouattara, 2009) and the adult male of Diane 2 (Fred) was supplanted by a new male (Ali) in October 2013 (E. Kane, Pers. Comm) with no long-term alteration of group's territory (C. Coye Pers. Obs, (Ouattara, 2009).

Table 1: Summary of group composition (adults only) in the four study groups. The name given between brackets is that of the male supplanting the first male present during the study period.

Species	Group	Name of the adult male	Number of adult females
Campbell's monkeys	Cam 1	Darius (Kili)	7
	Cam 2	Carlos	3
Diana monkeys	Diane 1	Omar	9
	Diane 2	Fred (Ali)	8

2.6.2. Observational data collection

Data were collected on wild groups of Campbell's and Diana monkey habituated to the presence of human observers. In both groups, the adult male and all the adult females were individually known. Identification was achieved by using morphological traits (*e.g.* body size, hairs coloration), scars and size of females' nipples.

Campbell's and Diana monkeys were followed by distinct observers: Karim Ouattara followed Cam 1 and Cam 2 during fifteen months between February 2006 and December 2007, with the help of a field assistant (Bertin Diero). I followed Diane 1 and Diane 2 for ten months between January 2013 and September 2014, with the help of a field assistant (Frédéric Mehon). We used similar observation protocols for both species. The observers first spent about 4 weeks habituating the monkeys to their individual presence and learning to identify adult group-members. Observations were then conducted during all-day follows of a group (from 7 or 8 am to 5pm) and the experimenter observed alternatively one group or the other every 3 days. Data collection included behavioural and vocal data and involved three complementary sampling methods: focal animal sampling for non-vocal behaviours and vocalisations, scan sampling of environmental and social variables and *ad libitum* sampling of rare events (*e.g.* male alarm calling, predator attacks). Karim Ouattara collected 230h of focal animal sampling on Campbell's monkeys and I collected 78h of focal animal sampling on Diana monkeys.

Focal animal sampling

Adult group-members were followed in pseudo-random order (*i.e.* when they could be identified and had not been observed less than 1h before). Focals lasted 15 minutes for Campbell's monkeys, but only 10 minutes for Diana monkeys as the latter use higher strata and tend to run more than Campbell's monkeys (about twice more during foraging bouts, McGraw, 2007) which made them harder to keep in sight for longer. Before any focal, the experimenter (*i.e.* K.O or C.C.) systematically took focal subject's identity, group's position in the territory, date, time as well as presence and distance of neighbouring conspecific and heterospecific groups. During focal sampling, we commented to describe subject's behaviour (including locomotion, foraging/feeding and posture), 'social' interactions (both intra- and inter-specific) and the identity (or species) of the interaction partner whenever possible as well as the distance and identity/species of any individual within 1m from the subject. The observer also commented on any unusual event susceptible to influence focal subject's behaviour (*e.g.* duiker fleeing, subject being spatially peripheral). In addition, the observer signalled every vocalisation emitted by the focal subject as well as the identity and order of intervention of vocal exchange partners (if any) whenever possible. Comments were recorded using a Lavallier microphone connected to a Sony TCD stereo recorder (K.O.) or to a Marantz PMD 660 recorder (C.C.). Vocalisations were recorded using a Senheiser ME88 (K.O.) or a Senheiser K6/ME66 (C.C.) connected to the stereo recorder.

Scan sampling

Scan sampling were conducted every thirty minutes. Both K.O and C.C. took group's position in the territory, the presence and estimated distance (in meters) of neighbouring conspecific groups as well as the presence and degree association of heterospecific groups. We coded this latter variable as follows: 0: the areas occupied by the groups overlap strongly, 1: partial

overlap (< 50% of surface) between the two groups, 2: groups are close from each other (< 25m) but not overlapping, 3: distance between groups is between 25 and 50 meters.

In addition, K.O. measured, for each visible group-member, individual's activity (*i.e.* foraging, travelling or resting), strata (*i.e.* on the ground, stratum 1: 1-5 m high, stratum 2: 5-15 m, stratum 3^-: 15 – 25 m high, stratum 3^+: 25 – 40 m, stratum 4: above 40 m) as well as the distance (m) and identity (or species if heterospecific) of the closest neighbour.

C.C. measured group spread (large: > 50 m or small: < 50 m), adult male's position in the group (*i.e.*: 0= in the middle; 1: peripheral, or x: unseen), sky 'cloudyness' (to assess brightness of the environment) and foliage density of each strata. Sky 'cloudyness' was coded on a decimal scale from 1 (clear blue sky, bright sun) to 3 (dark sky, fully cover in clouds with low visibility as when a storm is approaching). Foliage density was quantified as follows: 0 = no tree/branches at this stratum, 1: extremely dense foliage (*i.e.* impossible to see more than 30% of a monkey), 2: mildly dense foliage (*i.e.* possible to see 30-70% of a monkeys body), 3: scarce foliage (*i.e.* good visibility of most body parts of a monkey).

Ad libitum sampling

We noted (and recorded whenever appropriate) any unusual event susceptible to influence group's behaviour, even when it occurred while no focal sampling was conducted. Observers notably recorded and described group's reaction to leopards attacks (K.O.: N=3, C.C.: N=1), encounters with chimpanzees (K.O.: NA, C.C.: N=1), eagles attacks (K.O.: N=11, CC: N= 2) or eagles passing by (more than weekly), tree or large branches falling, fights (within- and between-groups), and any adult male calling bout (resident or neighbouring males).

2.6.3. Playback experiments

Playback experiments have frequently been conducted on wild populations of primates (Price, 2013; Slocombe, Townsend, & Zuberbühler, 2009; Wheeler, 2010), including in the Taï National Park. This method has proven its relevance (Zuberbühler & Wittig, 2011), notably to test receiver's reaction to context-specific vocalisations at the intra- and inter-specific level (Oda & Masataka, 1996; Rainey, Zuberbühler, & Slater, 2004; Zuberbühler, 2000b, 2002), or to make inferences about reasoning and mental representations (Cheney, Seyfarth, & Silk, 1995; Lemasson, Palombit, & Jubin, 2007; Zuberbühler, 2000a, 2000b; Zuberbühler, Cheney, & Seyfarth, 1999).

2.6.3.1. With unhabituated groups:

The aim of this experiment was to verify the suffixation pattern of Krak/Krak-oo calls of male Campbell's monkeys and its relevance to receivers. We performed playback experiments to wild unhabituated groups of Diana monkeys in an area of about 50km² around the CRE station. We broadcast series of natural and artificially recombined Krak and Krak-oo calls from two identified male Campbell's monkey recorded by Karim Ouattara between 2006 and 2007 in the Taï national park. Before each trial, we searched for a Diana monkey group by listening for their contact calls. When a group was spotted, we carefully approached the group after determining its position, direction and speed of travel. The playback and recording equipment were then silently positioned at 1.7 m above ground, 25–50 m away from the group, ensuring that the monkeys remained unaware of our presence. We used WAV files and broadcasts were conducted using a Philips GoGear Vibe player connected to a Nagra DSM speaker-amplifier and a Bose 151 Environmental speaker. Subjects' reaction was recorded with a Senheiser KE/ME66 directional microphone and a Marantz PMD660 recorder (sampling rate 44.1 kHz, resolution 16 bits, WAV sound format). To avoid retesting the same groups twice in short

succession, the GPS position was recorded using a Garmin map-62 after each trial, and we subsequently did not test any Diana monkey group in an area of 1 km^2 (twice the average home range size) around the location of the experiment for at least one month. Detailed descriptions of stimuli creation and playback protocol are provided in Chapter 3 (page 91).

2.6.3.2. With habituated groups

We conducted a playback experiment on a wild habituated group of Diana monkeys (Diane 2) in the Taï national park. The goal of the experiment was to test the combinatorial nature of female Diana monkeys' combined calls and relevance to receivers of changes in call's composition. We broadcast artificially recombined social calls of female Diana monkey involving call units recorded from group-members, from females in a neighbouring group (*i.e.* Diane 1) and from completely unfamiliar individuals living several kilometres away in the park. We followed the group daily and waited for the following conditions to be fulfilled before starting a trial: the group was not travelling or foraging 30 m or higher, there was no neighbouring group of Diana monkeys in the vicinity and no male loud calls had been produced for at least 15 min. Playback stimuli were broadcast from a Marantz PMD660 solid state recorder connected to a Nagra DSM speaker/amplifier and a Bose 151 Environmental speaker mounted on a telescopic perch. We recorded the behaviour of the subject for 30 s and group's vocal behaviour for 60 s following each trial, using a Senheiser KE/ME66 directional microphone and a Marantz PMD660 recorded (sampling rate 44.1 kHz, resolution 16 bits, WAV sound format). Detailed description of stimuli creation and playback protocol are provided in Chapter 4 (page 103).

2.7. Data analysis

2.7.1. Observational data

We analysed the observational data collected on the behaviour of female Campbell's monkeys, to characterise more precisely the context associated with the emission of simple (SH) and combined (CH) calls.

Data collected by Karim Ouattara, former PhD student in the EthoS Research lab, have been initially treated (*i.e.* excel coding of the focal and scan samplings, identification of calling bouts from focal individuals) by the same experimenter (K.O.). C.C., in collaboration with M. Arlet, postdoctoral collaborator has then performed the unification of data (*i.e.* putting together corresponding focals and scans) and analysed the type of calls uttered by the individuals as a function of the immediate environmental and behavioural context of their emission. We chose to include these two aspects as previous observations in Diana and Campbell's monkeys suggested that both subject's environment and behaviour impact call use by females (Candiotti et al., 2012a, 2012b; Ouattara, Zuberbühler, N'goran, Gombert, & Lemasson, 2009, Lemasson Unpublished data). Furthermore, we tested the influence of subject's socio-spatial integration within its group (assessed respectively through the average time spent grooming other group members and the average distance to the closest group-member) because previous studies showed an influence of social position in the group and social relationship on the vocal behaviour of captive Campbell's monkeys (Lemasson, Gandon, & Hausberger, 2010; Lemasson et al., 2005). We used non-parametric tests to determine which factors influenced the differential use of distinct (single and combined) calls in female Campbell's monkey. Analysis included variations in the rate of emission and variations in the proportion of calls given represented by each call type as these two approaches tackle distinct and complementary aspects of females' vocal behaviour. Detailed description of call classification, behavioural, environmental and acoustic data are provided in Chapter 4.

Data collected by C.C. on Diana monkeys have been partially processed only due to lack of time. They will be later included in a study aiming to clarify the dynamic of vocal interactions between adult females. Until now, this question could not be addressed because female Diana monkeys tend to spread over relatively large distances (*i.e.* 25 to 50m), and this prevented the systematic identification of exchange partners. We developed a tool that allows automated caller's recognition based on trained Artificial Neural Networks (ANN, see section 6 of this Chapter for more details). The data will be analysed using this new tool. In particular, we plan to analyse vocal interactions between individually-identified group members to determine whether females display preferential exchange partners and, if they do, whether the 'vocal dyads' correspond to the dyads showing high rates of grooming and proximity.

2.7.2. Experimental data

Subjects' reaction to both playback experiments (i.e. using male Campbell's monkey alarm calls and female Diana monkey social calls) were coded and analysed by C. Coye. We analysed the vocal reaction of the whole group for both playback experiments, and we also analysed detailed behavioural variables on individual subjects followed in focal sampling (*e.g.* direction and duration of gaze) for the second experiment. These variables were selected for their biological relevance on the basis of previous observations. Due to non-normal distribution, data were analysed using either Linear Mixed Models (Generalized or not: LMM and GLMM) or non-parametric multivariate analysis of variance (NPMANOVA). Detailed information about data analyses and statistical treatment are provided in Chapter 3 and 4 for the first and second playback experiment respectively.

2.7.3. Automated identification of caller using artificial neural networks

This procedure was developed in collaboration with Alexander Mielke (PhD student at the Max Planck Institute in Leipzig) and optimised for Diana and Campbell's monkeys' vocalisations by C. Coye. This work was conducted to develop an innovating tool that allows a detailed analysis of vocal exchanges and social partners involved in wild groups.

In addition, we used it to compare the performances of classification of the homologous CH and LA calls of female Campbell's and Diana monkeys (*i.e.* combined calls composed of a low-pitched quaver and an arched structure, see Chapter 6 of this thesis). The aim of this analysis was to determine whether combined calls in both species relate to caller's identity to the same extent (*i.e.* whether they allow similar classification performances when analysed with the same procedure). We will use this example to illustrate the principle and procedure developed for caller identification:

The procedure involved four sequential steps to (1) record and select call exemplars to be included in the Artificial Neural Network (from now ANN) training set, (2) extract the acoustic features of selected recordings using Mel Frequency Cepstral Coefficients (from now MFCCs), (3) train the ANNs for individual recognition and (4) testing classification performances. Step 1 was performed using Raven Pro 1.4, steps 2 to 4 were carried out using Matlab R2014b.

Step 1: Recording and selection of calls for the training set

We used recordings from wild female Diana and Campbell's monkey from habituated groups recorded respectively by C. Coye and K. Ouattara (see Methods section 4.1 and 4.2). C. Coye selected a set of high-quality recording from 3 identified females of each species for subsequent training of the ANNs. Training sets included 19 to 28 calls per individual (mean ± SE: 23± 1.57 calls). Calls selected had low background noise and no overlap with any experimenter's

voice or other vocalisations. We further restricted selection to a maximum of 9 calls recorded from the same call bout (*i.e.* within 15 minutes) to prevent identification biases due to recognition of background noise rather than individual calls. For each individual we took on average 2.6±0.43 (mean±S.E.) calls from the same call bout and used calls from 8.8±1.42 bouts. Recordings were cut as close to the call's edges as possible and we applied a low-pass filter at 12000 Hz to eliminate high-frequency sounds (mostly cicadas) without altering the calls, which top frequencies were always lower.

Step 2: Extraction of call's acoustic features

We extracted sounds acoustic features using Mel Frequency Cepstral Coefficients (MFCCs), which are widely used in automated speech and speaker recognition. Here, we aim to give a comprehensive and synthetic overview of the MFCC extraction process but detailed development of calculations and technical procedure for feature extraction are given elsewhere (Beigi, 2011; Cheng, Sun, & Ji, 2010; Rabiner & Juang, 1993).

The general principle is to extract the cepstral coefficients of a mel-transformed spectrum. For mel transformation, the spectrum's frequency axis is transformed from Hertz scale into mel scale using filter banks (32 mel-spaced triangular filters were involved) (Cheng et al., 2010). The idea underlying the "mel" scale is based on auditory perception of humans (and more generally of terrestrial vertebrates): our ear acts as a filter and concentrates more on certain frequency components. The key point being that those 'frequency filters' are not spaced uniformly, hence we do not perceive sounds linearly on all the frequencies of the audible range but perceive frequencies above 1000 Hz logarithmically (Volkmann, Stevens, & Newman, 1937). Transformation of a sound into mel scale (using 'filter banks') thus matches better

auditory perception of humans (and terrestrial vertebrates) than the more classical, linear Hertz scale and allows improved recognition (Deecke & Janik, 2006; Mielke & Zuberbühler, 2013).

The general principle of MFCC extraction is to slice the power spectrum in sections (*i.e.* frames) small enough to be statistically stationary. Each frame is then multiplied with a Hamming window and the Fast Fourier Transform (FFT) is computed. The frames are subsequently mel-scaled and the MFCCs are calculated by applying a discrete cosine transform to the energy from the frequency band filters (Logan, 2000).

In this analysis, the spectrum of each call was cut into seven frames of equivalent duration that were overlapping by two thirds (to prevent information loss from edge effect) (Clemins, Johnson, Leong, & Savage, 2005). Additional information regarding fine-tuned details of parameters and analysis we performed are available in Mielke & Zuberbühler, (2013) as we followed the exact same procedure for MFCC extraction.

Artificial Neural Networks: training

Artificial neural networks involve machine learning based on a principle similar to neurons in a brain. Neural networks consist of simple elements (neurons) connected with each other and that function in parallel. Various kind of neural networks exist, depending on the organisation of connections between the elements of the network. ANNs can be trained (*i.e.* supervised learning) to perform various operations including, but not restricted to, recognition tasks (Cheng et al., 2010; Mielke & Zuberbühler, 2013; Pozzi, Gamba, & Giacoma, 2010), clustering (Chon, Park, Moon, & Cha, 1996) or nonlinear statistical modelling with predictive purposes (Raman & Sunilkumar, 1995; Tu, 1996).

Here, the main idea was to provide ANN with "call exemplars" (more precisely, their acoustic features, expressed by MFCCs) as a training set. We provided 19 to 28 call exemplars from each of the 6 individuals (*i.e.* three Campbell's monkeys and three Diana monkeys) included in this preliminary study.

We used a cascade forward architecture (cascadeforwardnet() neural network in Matlab ®), which consists of three parts:

- an input layer, which size (*i.e.* number of neurons) corresponds to the size of the input vector computed during the feature extraction step. Here, we extracted 448 MFCCs for each call hence, input layer size was 448 neurons.
- an hidden layer composed of a fixed number of neurons decided prior to testing by trial and error optimization procedure. Here, we used 2 neurons only in the hidden layer to prevent overfitting.
- an output layer composed of the various classification outputs possible, here the number of individuals included in the analysis (*i.e.* 3 individuals as we tested Diana and Campbell's monkeys separately).

We used the 'trainbr' training function of Matlab ® (Bayesian regularization backpropagation training function). The maximum number of epochs (*i.e.* training iterations) was set to 1000. In addition, we used two complementary Input-Output processing functions: 'mapminmax' (which normalizes inputs and targets between -1 and +1) and 'mapstd' (which standardizes inputs and targets to have zero mean and unity variance). To determine when to stop the training, network's performance was measured, using the mean squared errors ('mse' performance function in Matlab ®), with normalization set to its standard value (*i.e.* normalizing errors between -2 and +2).

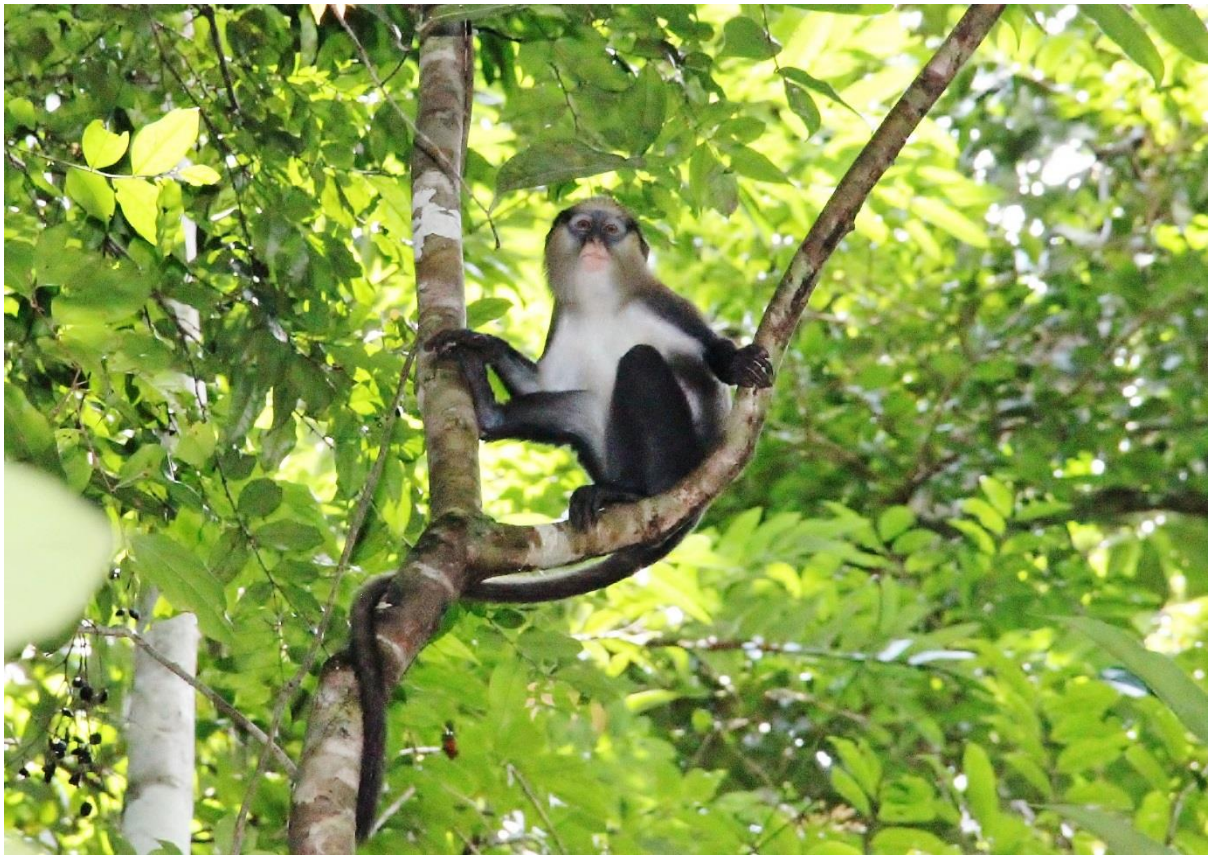
Artificial Neural Networks: testing

After training, the ANN classification performance was assessed on a test set composed of new call exemplars recorded from the same individuals but that were not included in the training set. We included four calls from each individual in the test set. To maximize classification efficiency, the training and testing procedures were repeated identically on several ANNs with similar architecture (here, 15 identical ANNs) and we used the averaged results of classification outputs from all the ANNs as the final result.

Tests were conducted separately on calls recorded from Diana (N=3 individuals) and Campbell's monkeys (N=3 individuals) as the goal was to determine whether the procedure allowed caller's identity among conspecific calls but not to train the networks for inter-specific discrimination (see pages 165-166 for some results and interpretation).

CHAPTER 3

SUFFIXATION INFLUENCES RECEIVERS' BEHAVIOUR IN NON-HUMAN PRIMATES



Summary of article 1

Question: In Campbell's monkeys from Taï National Park, males have a basic repertoire of six alarm calls - Boom, Krak, Krak-oo, Hok, Hok-oo and Wak-oo- that are emitted in context-specific sequences to warn group members about various threats in the environment. Previous observational studies suggested that a combinatorial vocal system may exist in these animals. Hence, while Krak call signal the presence of a leopard predator, it can be merged with an 'oo' suffix to create Krak-oo call that signals lesser urgent dangers (*e.g.* a duiker passing by).

The resemblance between these calls led authors to suggest that this system may rely on a suffixation process during which the addition of an 'oo' suffix decreases the urgency conveyed by the Krak stem. This is supported by the fact that the same combinatorial pattern is found with Hok calls, given to eagle predators, that can also be merged with the same 'oo' suffix in broader aerial contexts. But Krak and Krak-oo may also be two distinct calls, which just resemble each other to some extent independently from any combinatorial relation. In this case, the 'Krak' parts of these two calls might differ too much in their acoustic structures for the addition/deletion of a suffix 'oo' to change call's 'meaning' to receivers. **We conducted this study to determine whether the alarm call system of male Campbell's monkeys involves a suffixation process in which the presence or absence of an 'oo' unit plays a functional role.**

Method: To determine whether receivers based their reaction on the acoustic structure of the Krak stem or on the presence/absence of an 'oo' unit, we performed a playback experiment. We used natural Krak and Krak-oo calls, as well as artificially recombined calls obtained by adding an 'oo' unit to Krak calls or by deleting the 'oo' part of Krak-oo calls. The stimuli were broadcast to wild unhabituated groups of Diana monkeys in the Taï National Park, as the two species associate regularly and respond to each other alarm calls appropriately. In addition, while Campbell's monkeys would defend their territory against conspecific intruders, Diana monkeys do not react negatively to the presence of Campbell's monkeys in the vicinity. We analysed separately the vocal reaction of the adult male and that of the rest of the group (*i.e.* adult females and juveniles) to the four types of stimuli.

Results: Our results showed that the presence/absence of the 'oo' unit was the main factor explaining subjects' reaction, as receivers (both males and females) gave more calls and vocalised longer after hearing Krak than Krak-oo calls regardless of their origin (*i.e.* natural or artificial). The origin of the 'Krak' part (*i.e.* initially taken from a Krak or Krak-oo call) also influenced the number of calls given by the adult females and juveniles. We suggested that this variation resulted either

from distinct levels of caller's arousal during the initial recording of calls used, as stimuli since Krak calls were associated with more urgent contexts than Krak-oo calls, or from call's manipulation.

Conclusion: The strong impact of the presence/absence of an 'oo' unit confirmed the presence of a functionally relevant suffixation mechanism in the communication of Campbell's monkeys. However, the additional variations in receiver's behaviour in relation with the initial context of emission of the 'Krak' part of stimuli suggested a pattern of reaction more subtle than initially thought and that seemed to depend on both the vocal units involved and their fine acoustic structure.

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Suffixation influences receivers' behaviours in non-human primates

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ABSTRACT

Compared to humans, non-human primates have very little control over their vocal production. Nonetheless, some primates produce various call combinations, which may partially offset their lack of acoustic flexibility. A relevant example is male Campbell's monkeys, which give one call type ('Krak') to leopards, while the suffixed version of the same call stem ('Krak-oo') is given to unspecific danger. To test whether recipients attend to this suffixation pattern, we carried out a playback experiment in which we broadcast naturally and artificially modified suffixed and unsuffixed 'Krak' calls of male Campbell's monkeys to 42 wild groups of Diana monkeys. The two species form mixed species groups and respond to each other's vocalisations. We analysed the vocal response of male and female Diana monkeys and overall found significantly stronger vocal responses to unsuffixed (leopard) than suffixed (unspecific danger) calls. Although the acoustic structure of the 'Krak' stem of the calls has some additional effects, subject responses were mainly determined by the presence or absence of the suffix. This study indicates that suffixation is an evolved function in primate communication in contexts where adaptive responses are particularly important.

Keywords: Alarm calls, Syntax, Field experiment, Guenon

INTRODUCTION

Research on primate vocal behaviour continues to show surprising levels of complexity, both at the production and comprehension level [1]. The predation context has been a particularly rewarding source for new findings, probably because individuals are under strong selective pressure to use communication signals efficiently to protect genetic relatives and other valuable group members [2–4]. In some species, natural selection has favoured the evolution of acoustically distinct alarm calls with call variants related to the type of predator, the degree of threat or the appropriate anti-predator behaviour. Evidence is not restricted to primates but also includes a range of other taxa, including birds [5–7], non-primate mammals (prairie dogs (*Cynomys gunnisoni*) [8]; suricates [9]) and non-human primates (lemurs (*Lemur catta*) [10]; Old World monkeys (*Cercopithecoidae*) [11–14]; New World monkeys (*Platyrrhini*) [15–18]; apes (*Hominoidea*) [19]). Although these findings have been interpreted in terms of potential parallels to human language, animal alarm call systems usually lack flexibility, arbitrariness in acoustic structure and generativity, indicating profound differences between animal communication and human language [20–22]. Instead, animal communication tends to be very limited in the amount of acoustic variation available to the signaller to interact with others.

However, recent research has shown that there is another level of complexity in animal communication, in that some species combine basic acoustic units into more complex vocal structures. Such combinatorial abilities may have evolved in some species to partially offset their lack of flexibility in generating acoustic variation. Many bird and some mammal species have been observed to combine vocal units to produce more complex sequences [23–25] which in primates has been associated with differences in 'meanings' [26–30]. A particularly interesting example is the Campbell's monkeys' (*Cercopithecus campbelli*) alarm call system. Here, adult males have a repertoire of three basic alarm calls ('Krak', 'Hok', 'Wak'), which have been termed 'call stems', each of which can occur with an acoustically invariable 'suffix'

('oo') [31]. Here, we use the term 'suffixation' to refer to this phenomenon, the act of adding an acoustically invariable component to different call stems. In previous research we have found that suffixation appears to broaden the call's 'meaning' by, for example, transforming highly specific alarm calls ('Krak'), mainly given to leopards to general alert calls ('Krak-oo'), given to a wide range of events, including falling branches, interactions with neighbouring groups and other general disturbances [14,29,32].

The goal of this study is to test the 'suffixation' hypothesis experimentally, by testing whether the presence or absence of the suffix 'oo' in Campbell's monkey calls causes relevant differences in behavioural responses. To this end, we focused on the recipients by carrying out playback experiments with Diana monkeys (*Cercopithecus diana diana*). Diana and Campbell's monkeys regularly form mixed-species associations [33], coordinate their travel directions and attend to each other's alarm calls [12,34–36]. Although testing other Campbell's monkey groups would have been the obvious choice, we opted for testing Diana monkeys, mainly to avoid confounding effects of territorial behaviour. For example, it is likely that playing back Campbell's monkey calls triggered hostile responses towards the presumed intruder rather than quantifiable responses to the subtle acoustic differences generated by suffixation [14,33].

We created playback stimuli that consisted of natural 'Krak' and 'Krak-oo' calls and the corresponding artificially altered calls, *i.e.*, natural 'Krak-oo' calls with the 'oo' suffix deleted (artificial 'Krak' calls) and natural 'Krak' calls with an 'oo' suffix added (artificial 'Krak-oo' calls). We chose this design to rule out the possibility that there are subtle acoustic variations within the 'Krak' stem, depending on whether it was produced on its own or as part of a 'Krak-oo'. All calls were recorded from local male Campbell's monkeys. We predicted that if suffixation is communicatively relevant, then other monkeys should react according to the presence or absence of the suffix, regardless of the origin of the call stem. In particular, we

predicted that the animals would give more alarm calls and less affiliative calls to playbacks of natural and artificially edited 'Krak' calls than to playbacks of natural and artificially edited 'Krak-oo' calls.

MATERIAL & METHODS

Study site and subjects

Field experiments were conducted between May and July 2013 in Taï National Park, Ivory Coast, the largest preserved tropical rainforest in West Africa. The experimenter (C. Coye) and her field assistant conducted playback tests on unhabituated free-ranging groups of Diana monkeys, living in a roughly 50 km² area surrounding the C.R.E station (Centre de recherche en écologie, 5°50'N, 7°21'W). Diana and Campbell's monkeys are arboreal forest primates that live in small groups of one adult male and several adult females (Diana: 7-13, Campbell: 4-7) with their offspring. The density is about 2.5 groups per km²; with home ranges of about 56.0ha around the research station [33]. Although illegal, hunting has drastically decimated the population in other areas of the park. Diana and Campbell's monkeys form polyspecific associations on a daily basis, also with other sympatric primates [33]. Both male and female vocal repertoires are well described for both species [13,14,37,64,67]. The study has been conducted in accordance with the current laws in France, in Scotland and in Ivory Coast and has been approved by the University of St Andrews (School of Psychology) ethics committee and by the Ivorian Office of Parks and Reserves.

Playback stimuli

Structure of alarm calls may vary depending on the origin and identity of the caller [55,68,69] so we only used recordings from identified male Campbell's monkey from the general study area. Playback stimuli were edited from recordings made by K. Ouattara from two free-ranging

Campbell's males in Taï National Park, using Raven Pro 1.5, and were selected on the basis of recording quality, from a dataset classified by acoustic analysis for a previous study [32]. Playback stimuli consisted of vocal sequences of 1min (58.8s ± 0.95s; mean ± SE) with inter-call durations of 3s reflecting the natural structure of vocal sequences in this species [29,69]. Each male contributed with one sequence per playback category, resulting in eight sequences total: two natural 'Krak' call sequences, two natural 'Krak-oo' call sequences, two artificial 'Krak' call sequences (natural 'Krak-oo' from which the 'oo' suffix was deleted), and two artificial 'Krak-oo' call sequences (natural 'Krak' calls with an 'oo' suffix each added; Fig. 1). To ensure that subjects' reactions are due to the presence or absence of the 'oo' suffix, we created sequences by adding (artificial 'Krak-oo' sequences) or deleting (artificial 'Krak' sequences) 'oo' parts to the calls used to create the sequences of natural stimuli. All 'oo' suffixes added came from natural 'Krak-oo' calls from the same males. The calls were processed with a low-pass filter to remove high frequency background noise (above 16 kHz, above the frequency range of the male calls, Fig. 1). Calls were amplified to obtain a naturalistic intensity of around 90db at 1 metre from the speaker.

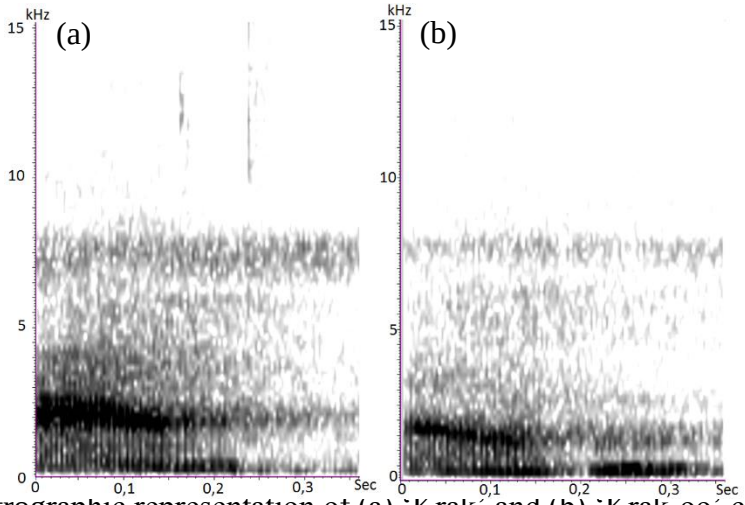

Figure 1: Spectrographic representation of (a) `Krak´ and (b) `Krak-oo´ calls.

Experimental protocol

Thirteen trials were conducted in a random order for each stimulus category, with never more than four trials per day. None of the Diana monkey groups studied were habituated to human presence and the exact location of their home ranges were unknown. To avoid retesting the same groups twice in short succession, the GPS position was recorded using a Garmin map-62 after each trial, and we subsequently did not test any Diana monkey group in an area of $1km^2$ (twice the average home range size) around the location of the experiment for at least one month. Each stimulus category was never played more than once at the same location.

For each trial, the experimenters searched for a Diana monkey group by listening to their contact calls. The playback and recording equipment were then silently positioned at 1.7 meters above ground, 25-50 meters away from the group, ensuring that the monkeys remained unaware of the experimenters' presence. Unhabituated Diana monkeys produce alarm calls to humans and sometimes approach and stare at observers, so detection is easily recognised. Playback stimuli were broadcast with a Philips GoGear Vibe player connected to a Nagra DSM speaker/amplifier and a Bose 151 Environmental speaker. Recording equipment consisted of a Sennheiser K6/ME66 directional microphone and a Marantz PMD660 solid-state recorder (sampling rate 44.1 kHz, resolution 16 bits, WAV sound format). Before each stimulus presentation, the experimenters waited at least 15 min to ensure that the male had not produced any loud calls and that the group had not noticed our presence, otherwise the trial was discarded.

Dependent variables

The vocal response of the study group was recorded and analysed for both the adult male and the females with their offspring. Diana monkeys show strong sexual dimorphism in vocal behaviour; the calls of the adult males are very different compared to calls given by the females

and immature group members [67]. Hence, we analysed separately male alarm calls – taking into account the total call bout given- and the groups call rates. The latter were analysed for five minutes following the start of each playback since previous work has shown that, after this time, individuals have usually returned to their baseline call rates, regardless of stimulus type [34].

We counted the total number of alarm calls given by the adult male, and the total number of calls given by the group, classified as four 'social' call units (H, L, R, A) and two 'alarm' call units (Alk, W) [37] (Figure showing vocal repertoire of female Diana monkeys in the Electronic Supplementary Material). Female alarm call units are given only to disturbances but never in peaceful contexts (C. Coye 2013, unpublished data). The six basic call units can be combined into five combined call types (HA and LA social positive calls, RA alert calls, RAlk and RW alarm calls) [37]. 'Social' call units are part of calls given in affiliative and peaceful situations (H, L, A). To obtain reasonable sample sizes while respecting biological saliency, we discriminated the following call types and units: Alk call units combined or not to an R call (hence forming the "Alk+RAlk" alarm group), W call units combined or not to an R call ("W+RW" alarm group), R and RA alert calls (lumped together under the name RA in this analysis), and lumped all social calls (H, L, A and combinations between them) into one group, which led to the following sample sizes: $N_{Alk+RALK}$= 2488, N_{W+RW}=1136, N_{RA}= 458, N_{HLA}= 973. For each trial, we also recorded the group's latency to give their first call. All groups responded with calls to the playback stimuli. Finally, we measured the time spent in 'alert' by the group, defined as when more than five alarm units or calls (Alk, W, RAlk, RW or RA) were produced over 30s.

For the males, we measured the total duration of each call bout (time between the first and last call), when a male did not call a call bout duration equal to zero was attributed. Finally, we measured the latency to give the first call. In some trials (N=7), the male did not call, in which

case we assigned a dummy latency of 128.8s, corresponding to twice the maximum observed latency to call for all males.

Statistical analysis

We considered each playback as an independent event. Among the 52 playback trials performed, 10 were excluded due to equipment failure or because of early detection of the experimenters or the equipment, which generated a final sample size of N=11 natural 'Krak' [K], N=12 natural 'Krak-oo' [K_{+}], N=9 artificial 'Krak' [$K_{( )}$] and N=10 artificial 'Krak-oo' [$K_{(+)}$].

We tested the impact of both the origin of the 'Krak' part of calls (taken either from a 'Krak' or from a 'Krak-oo' call) and the presence of an 'oo' suffix in the calls, for each variable described. To this end, we used a Generalised Linear Mixed Model (GLMM) with a Poisson distribution and a log link or a Linear Mixed Model (LMM) with a Gaussian distribution and an identity link, using the glmer( ) and the lmer( ) function from the 'lme4' R package, respectively. We systematically used GLMMs to analyse the number of calls produced and LMMs to analyse the duration of calling and alert as well as the latency to give the first call (separately for the adult male and the rest of the group).

For both GLMM and LMM we included the origin of the 'Krak' stem (*i.e.* taken from a natural 'Krak' or from a 'Krak-oo' call) and the presence of an 'oo' suffix as crossed fixed factors. The identity of the Campbell's monkey call producer was entered as a random factor (two males). Then, we performed an Analysis of Variance (Anova), using the Anova( ) function from the 'car' R package, running type II Wald Chi² tests to study the effect of the fixed factors.

In some analyses the origin of the 'Krak' stem and the presence of the suffix both had a significant impact. To compare the relative influence of these two factors, we carried out two

additional GLMMs (distribution: Poisson, link: log) and LMMs (distribution: Gaussian, link: identity), using the glmer( ) and lmer( ) functions of the 'lme4' R package. All models included caller identity as a random factor but only one of the two possible fixed factors, either the origin of 'Krak' stem or the presence of suffix. We then compared the respective corrected Akaike Information Criterion (AICc) for both models and considered the one with the lower AICc to be significantly more accurate, provided the absolute value of the difference between the two AICc (*i.e.* |Δ(AICc)|) was greater than two [70,71]. All statistical tests were computed with R 3.0.2.

RESULTS

Call rates

We tested 42 different groups of Diana monkeys with the four different playback conditions, *i.e.*, natural 'Krak' (N=11), natural 'Krak-oo' (N=12), artificial 'Krak' (N=9), and artificial 'Krak-oo' (N=10). We analysed the number of calls given by Diana monkeys after each playback using a Generalised Linear Mixed Model (GLMM, model 1). As predicted, male Diana monkeys gave significantly more alarm calls after hearing 'Krak' calls (natural or artificial) than 'Krak-oo' calls (natural or artificial; Fig. 2), while the acoustic structure of the 'Krak' stem had no significant impact (Table 1). Diana monkey females gave more alarm calls and fewer social calls after hearing 'Krak' than 'Krak-oo' calls (natural or artificial; Fig. 2), but we also found that the acoustic structure of the 'Krak' stem had an additional impact. We thus carried out two more GLMMs (models 2 & 3) and compared the corrected Akaike Information Criterion (AICc) obtained for the two models. The difference between AICc values was greater than 2 for all variables, and the lower AICc value was obtained systematically if the model included 'suffix' as the only fixed factor (Table 1). This indicates that the presence of the suffix was the main factor to explain female call rates (see §4e for more details).

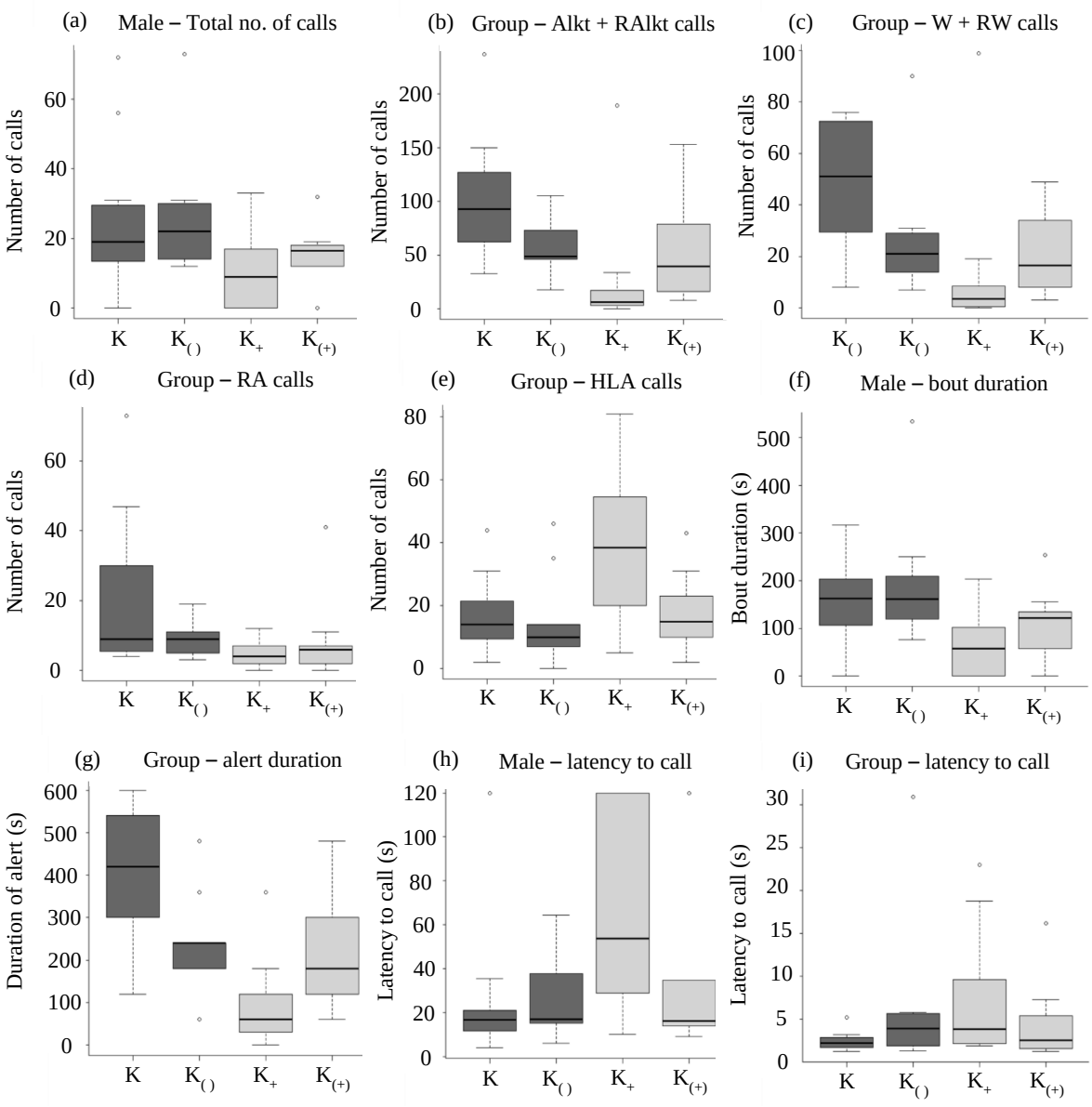

Figure 2: Median and inter-quartile range in the four experimental conditions natural 'Krak' (K, N=11), artificial 'Krak' ($K_{(\ )}$, N=9), natural 'Krak-oo' (K_{+}, N=12), and artificial 'Krak-oo' ($K_{(+)}$, N=10) for each variable studied. Plots (a) to (e) show the number of calls given respectively by the male (a) and by the group with (b) 'Alk' alarm call units -given alone and combined with an R unit-, (c) 'W' alarm call units -given alone and combined with an R unit-, (d) number of 'RA' alert call given (combination of "R" and "A" call units) and (e) sum of three positive social call units and combinations between them (*i.e.* H, L, A call units and HA and LA calls). Plots (f) and (g) show the duration of alarm respectively for the male and the group. Finally, plots (h) and (i) show latency to give first call respectively for the male (h) and the group (i).

Calling durations

We compared the duration of the males' alarm calling and the rest of the groups' alert calling across conditions using Linear Mixed Models (LMMs). As predicted, playbacks of 'Krak' calls

elicited longer responses in both measures than 'Krak-oo' calls, regardless of whether they were natural or artificial (Fig. 2). In our models, male alarm call duration was significantly explained by the presence of the suffix alone while the groups' alert call duration was explained by both suffixation and the structure of the 'Krak' stem (Table 1). As before, we compared two more LMM models (models 2 & 3). Again, the difference between their AICcs was >2, which showed that the model with the lower AICc –corresponding to the third model (with suffixation only) - contained the factor having the main impact on the monkeys' behaviour. This hence indicated that the presence of suffix was the main factor to drive alert duration (Table 1).

Latencies to first calls

Finally, we analysed the males' and the groups' latencies to give first calls (Fig. 2). Here again, suffixation was the only significant factor to explain the male's latency to call but for the groups' latencies to call, we found no significant effects (Table 1).

Table 1: (a) Results of the GLMM and of the Δ(AICc) analysis for each number of calls given by the subjects. (b)Results of the LMM and of the Δ(AICc) analysis for males' bout duration, groups' alert duration and for males' and groups' latency to give first call. Tables show Chi² and p values from the first model (i.e. GLMM-1 or LMM-1) for each of the two fixed factors included in the model (i.e. origin of the 'Krak' stem and presence of an 'oo' suffix). Significant p-values (under 0.05) are in bold. Tables show as well the AICc values of the second and third models and the absolute value of the subtraction between these two AICcs: |Δ(AICc)|. The lower AICc value, which corresponds to the main parameter explaining the results, is in bold.

(a)		'Krak' stem		suffixation		AICc 'stem'	AICc 'suffix'	|Δ(AICc)|
Emitter	Call type	Chi²	p-value	Chi²	p-value			
Male	Alarm	2.87	> 0.05	82.85	< **0.0001**	-	-	-
Females	Alk + RAlk	219.09	< **0.0001**	312.25	< **0.0001**	1817.49	**1718.86**	98.63
	W + RW	71.53	< **0.0001**	167.03	< **0.0001**	1114.24	**1008.95**	105.29
	RA	50.87	< **0.0001**	66.61	< **0.0001**	614.80	**596.98**	17.82
	HLA	44.00	< **0.0001**	52.87	< **0.0001**	736.08	**722.16**	13.92

(b)		'Krak' stem		suffixation		AICc 'stem'	AICc 'suffix'	|Δ(AICc)|
Emitter	Variable	Chi²	p-value	Chi²	p-value			
Male	Bout duration	0.028	> 0.05	10.13	< **0.01**	-	-	-
	Latency to call	1.86	> 0.05	6.45	< **0.05**	-	-	-
Females	'Alert' duration	12.04	< **0.001**	21.32	< **0.0001**	549.84	**543.26**	6.58
	Latency to call	3.32	> 0.05	0.49	> 0.05	-	-	-

DISCUSSION

With this study, we demonstrated experimentally that suffixation is a salient acoustic feature in Campbell's monkey vocal communication. As predicted, Diana monkeys reacted more strongly to 'Krak' calls (usually indicating leopard presence) than to 'Krak-oo' calls (indicating a general threat). Diana monkeys consistently produced more alarm and fewer social calls, gave first call earlier, called and remained vigilant for longer after hearing unsuffixed -'Krak'- calls (natural or artificial) than suffixed -'Krak-oo'- calls (natural or artificial, Fig. 2). Overall, the presence or absence of the suffix was the only parameter that had a systematic and sustained effect on Diana monkey responses, suggesting that the 'oo' suffix is communicatively relevant in that 'Krak-oo' calls are a combination of a 'Krak' stem with an 'oo' suffix.

These findings are novel because previous animal communication studies have only reported combinatorial abilities at the sequence level. Although there are a few examples of combinatorial phenomena at the call unit level [37,38] we are not aware of any study that has investigated experimentally whether this is communicatively relevant to recipients [39]. The only comparable studies with non-human primates have focussed on discrimination and categorisation abilities of grammatical rules in human speech or artificial grammars [40–42], but never as part of the animals' own natural communication systems. Our study thus

demonstrates experimentally that suffixation can be communicatively relevant in the natural vocal communication of free-ranging, untrained animals in biologically relevant contexts.

Reactions to natural and artificial 'Krak' calls were more similar to each other than reactions to natural and artificial 'Krak-oo' calls, perhaps because artificially adding 'oo' parts to existing 'Krak' calls was technically more challenging than deleting the 'oo' from 'Krak-oo' calls. This may have led to less naturally sounding stimuli for artificial 'Krak-oo' than 'Krak' calls, a difference that may have been perceived by the Diana monkeys. Although suffixation had the strongest effect on the monkeys' behaviour, the acoustic structure of the 'Krak' stem (*i.e.*, whether playback stimuli were created from natural 'Kraks' or natural 'Krak-oo' calls) also had a significant impact on some female response variables (Table 1). It is also clear that the presence of a leopard (a reliable trigger of male 'Krak' calls) represents a different psychological experience than hearing the sounds of a falling tree (a reliable trigger of male 'Krak-oo' calls). These differences in perceived danger and urgency appear to have left acoustic traces in the calls' structure, a mechanism suggested by several authors [31,43,44]. Our results demonstrate that Diana monkeys perceived these subtle acoustic differences in the 'Krak' stem although they relied more on the presence or absence of the suffix in their responses (Fig. 2).

How exactly such findings should be interpreted, especially what types of internal states are involved in callers and recipients is the topic of an ongoing debate [45–51]. Some authors prefer to invoke notions related to human-like emotions, while others offer more cognitive interpretations. For example, one prominent theory proposes that the calls' acoustic structure directly affects recipient arousal, without much intervening processing [52]. Another view is that monkeys form associations between acoustic structures and the corresponding external events that trigger them, to the effect that acoustic structures become carriers of meaning [53]. A third view is that animals interpret acoustic information in relation to the current context,

which is based on evidence that the same calls can trigger different reactions depending on the current context [54,55].

We are not able to contribute much to this discussion with our current data. On the one hand, previous studies with Campbell's monkeys have shown a direct correlation between acoustic structure and the external events that triggered them, as well as adequate recipient responses to experimentally presented exemplars of calls [14,31,32,56] in line with a 'semantic' interpretation. On the other hand, some of the Campbell's monkey calls may contain specific acoustic features that have a direct impact on the recipients' nervous systems, as proposed by Owren & Rendall (2001). For instance, sharp onsets in alarm calls may enhance levels of internal arousal and thus trigger movement. In our case, this is a less likely explanation because although both 'Krak' and 'Krak-oo' calls share the sharp onset, only 'Krak' calls elicited strong behavioural reactions. In another study, 'boom' calls (a natural indicator of non-predatory contexts) were artificially added to Campbell's monkey alarm calls, which also had a significant effect on behavioural responses [14,26]. Nevertheless, what internal states, if any, are causally responsible for mediating between calls and reactions will need to be investigated by other, more targeted research.

This experiment also provides further evidence for complex interspecific communication, with Diana monkeys demonstrating surprising discriminative skills when exposed to the calls of another species. We consider it likely that similar interspecific communicative abilities are also present in other species, in line with the idea that polyspecific primate groups are more than mere assemblies of different groups to avoid predators but instead form supra-social organisations with animals interacting with each other on a daily basis as individuals [33,57]. So far, interspecific communication has been largely found in the predation context, in some cases between predator and prey. For example, Diana monkeys also distinguish between some of the calls of one of their predators, the chimpanzees [58], between the different alarm call

types produced by sympatric putty-nosed monkeys [36] or between the alarm calls of different species of guinea fowl [54]. These perception abilities are most likely a consequence of the frequent associations of Diana monkeys with other primate species and observing predator-prey interactions in other species, suggesting that similar abilities exist in other primates.

Finally, the suffixation mechanism described here is unlikely to be an isolated phenomenon in primate communication. Related work on female Diana monkeys vocal communication has shown that the contact calls of adult females also consist of acoustically distinct elements that are combined in structured ways with likely effects on the information they may convey [37,59]. In other work, female Campbell's monkeys were found to combine two social call units to convey information associated with arousal [44] and social bonds (affiliated females produce a second unit with similar frequency modulation shapes) [60]. In red-capped mangabeys (C*ercocebus torquatus*), both sexes produce context-specific combinations of call units in sex-specific ways, while contextually similar call types are produced in sequences, with length and complexity depending on the vocal activity of other group members [61]. Although these phenomena require more rigorous experimental testing, they suggest that affixation is a widely present feature of non-human primates' communication. The more general hypothesis is that vocal complexity (as seen in combinatorial systems) is the evolutionary outcome of social complexity [61–65] , suggesting that similar phenomena should be found in other species with complex social demands, notably some of the great ape species.

Further research is needed to get a deeper understanding of these combinatorial mechanisms within different primate calls. For Campbell's monkeys, the observed vocal combinations effectively enlarge their vocal repertoire, despite these animals' limited articulatory control. Future research will have to focus on the differences in perceived meaning of the other combinations that have been found in natural communication, notably between 'Hok' and 'Hok-oo' and between 'Wak' and 'Wak-oo' calls, to determine whether suffixation

consistently changes relatively specific messages to more general ones, as suggested by Ouattara et al. (2009). Findings will be of interest because they suggest that basic features of human speech, such as duality of patterning [66], can evolve independently in species that are not so closely related to humans.

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DATA ACCESSIBILITY

The dataset supporting this article can be downloaded from the University of Rennes 1, Home document repository: https://ecm.univ-rennes1.fr/nuxeo/nxdoc/default/1b1b9b09-5dea-48d4-a071-ec236297db27/view_documents. All statistical tests were computed using the R software which can be downloaded at http://cran.r-project.org/bin/windows/base/

AUTHORS' CONTRIBUTION

All authors contributed to this work equally: A.L. and K.Z. gave financial support to this project; all authors developed the concept and designed experiments. K.Z., K.O and C.C.

organized the field mission to Ivory Coast, C.C. and K.O performed the experiment and collected the data and stimuli. All authors worked on data analysis and prepared the manuscript.

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CHAPTER 4

MORPHOLOGICALLY STRUCTURED VOCALIZATIONS IN FEMALE DIANA MONKEYS

Summary of article 2

Question: Female Diana monkeys possess in their vocal repertoire three acoustically distinct social call types L, R and A. L and R are associated with distinct emotional contexts of emission (neutral/positive contexts *vs* negative/discomfort contexts respectively). The arched (A) call is found in all possible contexts, but varies acoustically between females, with hence a high potential for identity coding. The calls can further be merged non-randomly into LA and RA combined calls. The combined calls resulting from this combination are given in contexts that depend on the context associated with their introductory unit. Based on observational data, authors proposed that combined calls convey linearly the information from the units which compose them. **We thus conducted this study to test experimentally whether the contact call system of female Diana monkeys has a morphology-like organisation. In other words: does it implies the linear combination of call units into combined calls which information content varies with their component?**

Methods: We performed a playback experiment on eight adult females in a habituated group of wild Diana monkeys. To verify the combinatorial nature of the combined contact calls, we used artificially recombined stimuli composed of call units initially uttered separately. To determine the relevance to receivers of the contextual introductory unit, we compared subjects' reaction to the broadcast of stimuli created by merging L or R contextual units (recorded from callers unfamiliar to the subjects) with A calls from a group member (*i.e.* respectively LA_G and RA_G stimuli). To determine whether A calls allowed receivers to identify the caller, we compared subject's reaction to stimuli created by merging the same R units with either A calls from group members or A calls from females in a neighbouring group (*i.e.* RA_G and RA_N stimuli). Each of the eight subjects was tested with a unique set of three stimuli (*i.e.* LA_G, RA_G and RA_N). We recorded subject's locomotion, gaze direction and duration as well as group's vocal reaction after each playback.

Results: Subjects displayed distinct patterns of reaction to the three types of stimuli, which varied according to the units composing them. Subjects spent more time vigilant (latency to move, environment scanning), while the group emitted more isolated (non-exchanged) calls, after the playback of RA_G (*i.e.* negative) compared to LA_G (*i.e.* positive) stimuli. In addition, subjects displayed decreased locomotion (with less time spent walking and increased latency to walk) and a strongly altered gazing pattern (staring at the speaker) after hearing RA_N (non-group members) compared to RA_G (group members) stimuli.

Conclusion: Our results confirmed the relevance of both contextual and identity units to conspecific receivers and strongly suggests the existence of a morphologically-structured combinatorial system in the vocal repertoire of female Diana monkeys.

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Morphologically structured vocalisations in female Diana monkeys

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ABSTRACT

Social complexity is often thought of as a driving force in the evolution of communication and cognition, but this is at odds with the fact that non-human primates generally display only very limited flexibility in vocal production. Some primates partially overcome their limited vocal flexibility by combining two or more acoustically inflexible calls into complex sequences. Equally relevant is that some primate calls consist of separable morphological elements whose combinations create different meanings. Here, we focus on the vocal system of wild female Diana monkeys (*Cercopithecus diana diana*), who produce three call units (R, L, A) either singly or merged as RA or LA call combinations. Previous work has shown that R and L convey information about external events, while A conveys information about caller identity. We tested this hypothesis experimentally, by broadcasting artificially combined utterances to eight adult females. To test the significance of the R and L 'event' units, we merged them with the A 'identity' unit of a group member. To test the significance of the 'identity' unit, we merged an R 'event' unit with an 'identity' unit from a group member or a neighbouring individual. Subjects responded in ways that suggested that both event and identity units were relevant, suggesting that Diana monkeys' social calls possess morpho-semantic features. We discuss this finding in relation to the co-evolution of communication and social complexity in primates.

Keywords: acoustic playback, call combination, field experiment, guenons, morphology, social communication

INTRODUCTION

The evolution of vocal complexity in animals appears to be largely driven by social complexity as well as by visually difficult and ecologically challenging habitats (Bouchet, Blois-Heulin, & Lemasson, 2013; Dunbar, 1993; Dunbar, 1998; Marler, 1967; McComb & Semple, 2005). Many vertebrates and most primates live in social groups with complex and dynamic social networks and long-term bonds (de Waal, 1987; Lehmann, Korstjens, & Dunbar, 2007; Wrangham, 1987). As a result, primates are constantly challenged to maintain cohesion during travel and other activities to optimise foraging, to compete with neighbouring groups and to protect themselves against predators (Dunbar & Shultz, 2007; Lehmann et al., 2007; van Schaik, 1983; van Schaik & van Hooff, 1983). To this end, many species evolved specific vocalisations to maintain cohesion and synchronise within-group activities (Gautier & Gautier, 1977; Oda, 1996; Uster & Zuberbühler, 2001). Calls are often individually distinct and function to advertise individual identity or membership to specific social units (Bouchet, Pellier, Blois-Heulin, & Lemasson, 2010; Crockford, Herbinger, Vigilant, & Boesch, 2004; Dunbar, 2003; Neumann, Assahad, Hammerschmidt, Perwitasari-Farajallah, & Engelhardt, 2010; Rendall, Rodman, & Emond, 1996).

In light of this, it is surprising that non-human primates are thought to have relatively limited, species-specific vocal repertoires with a fixed set of call types that remain largely unchanged throughout adult life (review by Bouchet et al., 2013) and little signs of flexibility or voluntary control in call production (Hammerschmidt & Fischer, 2008). However, a more recent line of research has continued to demonstrate a previously under-described source of communicative complexity, namely the ability of individuals to assemble fixed acoustic units of their repertoire into more complex utterances. There is now good evidence that several non-human primate species produce calls in non-random sequences, with the information changing depending on

the order or temporal structure of call sequences (vervet monkeys *Cholorocebus aethiops*: Seyfarth, Cheney, & Marler, 1980; Campbell's monkeys *Cercopithecus Campbelli*: Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010; Ouattara, Lemasson, & Zuberbühler, 2009a; Zuberbühler, 2001; white-handed gibbons *Hylobates lar*: Clarke, Reichard, & Zuberbühler, 2006; bonobos *Pan paniscus* and chimpanzees *Pan troglodytes*: Clay & Zuberbühler, 2011; Slocombe & Zuberbühler, 2005; Diana monkeys *Cercopithecus diana diana*: Zuberbühler, 2000). One argument has been that these combinatorial capacities evolved in primates to enable more complex communication (Zuberbühler & Lemasson, 2014).

So far, however, most examples of call combinations are from studies on male primate alarm calls, which is surprising because social events may be at least as complex as dealing with predator encounters. Hence, if complex vocal abilities have evolved to deal with social complexity, we should find combinatorial phenomena in vocal behaviour during social interactions and also in females, the social core of primates species (Buzzard & Eckardt, 2007; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987).

One particularly promising candidate is the contact call of some forest living female guenons. In Campbell's monkeys, for instance, adult females produce a short, low-pitched contact call, either as a single unit or merged with a second long, arched, and frequency-modulated unit to form multi-unit utterances (Lemasson & Hausberger, 2011). The acoustic structure of the first unit varies depending on the degree of arousal experienced by the caller (Lemasson, Remeuf, Rossard, & Zimmermann, 2012) and contains fewer identity cues than the second, arched unit, which strongly relates to the caller's identity (Lemasson & Hausberger, 2011; Lemasson, Hausberger, & Zuberbühler, 2005; Lemasson, Ouattara, Petit, & Zuberbühler, 2011). The

second unit is never uttered alone but functions as an affixation to the first unit, which can also be uttered alone.

A second relevant example is the contact calls of female Diana monkeys, an arboreal forest-dwelling primate living in groups of one adult male and seven to thirteen adult females with their offspring (McGraw, Zuberbühler, & Noë, 2007). As in most primates, the females are the philopatric sex and constitute the social core of the group (Candiotti et al., 2015). They produce, amongst others, three acoustically distinct social calls (L, R and A) depending on context (Candiotti, Zuberbühler, & Lemasson, 2012a, 2012b; Uster & Zuberbühler, 2001): L calls are mostly given in socio-positive and neutral events (e.g., foraging, affiliative interactions). R calls are mostly given in socio-negative events and mild danger (e.g., conflict within or between groups, walking on the ground), suggesting that these calls relate to the external events or emotional valences experienced by the caller. A calls, finally, are produced in unspecific ways to a large variety of events, but here the acoustic structure varies substantially between individuals, suggesting they function to signal the caller's identity, similar to what has been found in Campbell's monkeys. The three call types can be emitted alone (A, L, R) or merged as two combined utterances, either LA, or RA. Combined structures thus contain information about the external event (L or R) and the caller's identity (Candiotti et al., 2012a, 2012b), with some interesting parallels to the function of morphemes in human speech (Collier, Bickel, Schaik, Manser, & Townsend, 2014; Hurford, 2008; Tellier, 2008; Veselinovic, Candiotti, & Lemasson, 2014).

Here, we tested experimentally whether the information conveyed by complex calls of Diana monkeys is compositional, i.e., whether the combined calls relate linearly to the information conveyed by the units given singly, as suggested by Candiotti et al.'s (2012a) observational data. To this end, we broadcast artificially combined calls to different subjects, eight female

Diana monkeys belonging to a study group habituated to human presence. We created experimental stimuli by manipulating either the initial or final call unit using recordings from group members, neighbours and completely unfamiliar individuals. Our goal was to test the significance of the L and R 'event' and A 'identity' units. To this end, we merged L and R units with A 'identity' units from familiar group members or neighbouring individuals. We predicted that, if combinations of call units were meaningful to receivers, L and R units should cause significant behavioural differences, particularly in terms of vocal responses, vigilance and exploratory behaviours. Because Diana monkeys are highly territorial, we also predicted different behavioural responses to identity-encoding A units, depending on whether they originated from a group member or neighbour.

MATERIAL AND METHODS

Study site and subjects

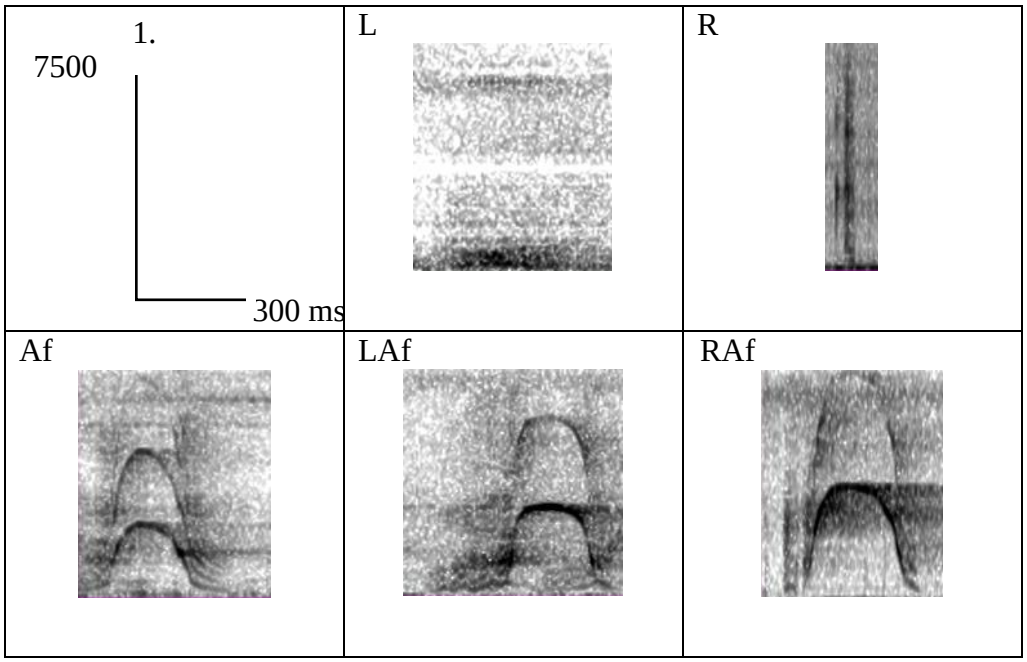
Field experiments were conducted between June and September 2014 in Taï National Park, Ivory Coast (5°50'N, 7°21'W). The experimenter (CC) and two field assistants (FB and FG) conducted playback experiments in a free-ranging group of Diana monkeys (*Cercopithecus diana diana*) with individually known subjects habituated to human presence for more than twenty years. At the time of the experiments, the group consisted of one adult male and eight adult females with their offspring. The experiment involved all the adult females of the habituated group.

Playback stimuli

All calls (stimuli and subject's reaction to the playbacks) were recorded using a Sennheiser K6/ME66 directional microphone connected to a Marantz PMD660 recorder (sampling rate 44.1 kHz, resolution 16 bits, WAV sound format) in Taï National Park. Calls from group

members were recorded in May 2014; calls from unfamiliar and neighbouring Diana monkeys were recorded in June-July 2013 and February-June 2010. All calls were recorded under similar environmental conditions and distances to ensure high quality, low background noise, and no overlap with any other sound.

When creating the playback stimuli, we followed Candiotti et al., (2012a) classification (Fig. 1), who define L call units as continuous low-pitched trills with a general ascending frequency modulation (duration±*SD*: 409±106 ms, Minimum fundamental frequency±*SD*: 247±84 Hz, Maximum fundamental frequency±*SD*: 654±354 Hz), R call units as rapid repetitions of one to four short atonal units separated by brief periods of silence (duration±*SD*: 82±29 ms, Minimum fundamental frequency±*SD*: 331±170 Hz, Maximum fundamental frequency±*SD*: 429±199 Hz, First unit duration±*SD*: 28±11 ms, First inter-unit silence±*SD*: 46±18 ms) and A call units as tonal, arch-shaped frequency modulations (duration±*SD*: 298±105 ms, Minimum fundamental frequency±*SD*: 324±233 Hz, Maximum fundamental frequency±*SD*: 3090±696 Hz).



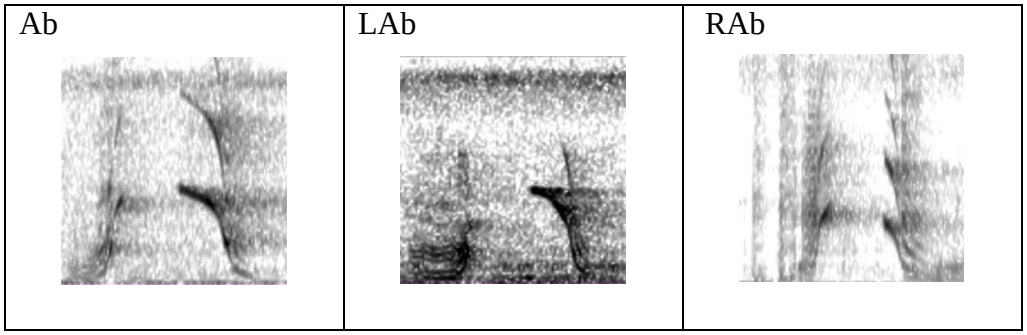


Figure 1: A, L and R call exemplars from female Diana monkeys emitted alone or merged into combined calls LA and RA (Ab and Af being two sub-types of A call).

We created twenty-four different playback stimuli to generate the following three categories (Fig. 2): LA_G: combination of an unfamiliar individual's L merged with an A from an adult female group member (*N*=8); RA_G: combination of an unfamiliar individual's R merged with an A from an adult female group member (*N*=8); RA_N: combination of an unfamiliar individual's R merged with an A from an adult female from a neighbouring group (*N*=8).

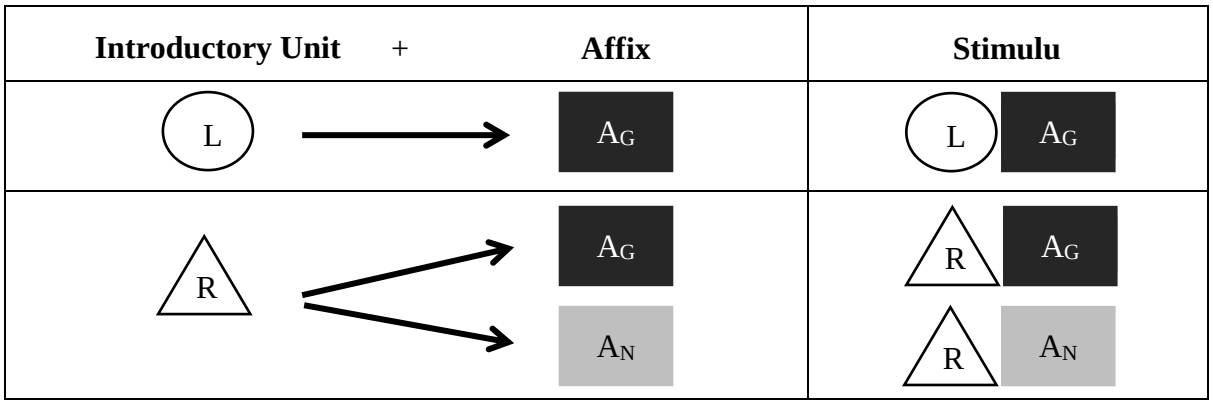


Figure 2: Stimulus creation. The geometric shapes indicate the valence of the call. Circle and triangle represent context-dependent units, respectively L (associated with positive and neutral events) and R (associated with negative events). Rectangles represent identity-dependent units A. The shading indicates the origin of the call recorded: white: unfamiliar individuals; black: group-members; grey: neighbouring individuals.

Each of the eight subjects received its own set of LA_G, RA_G and RA_N call combinations. Within a given set, we systematically used the same R call unit and the same A call unit to create paired stimuli (i.e., L**A**$_G$-R**A**$_G$ and **R**A$_G$-**R**A$_N$) to allow the comparison of the changes in subject's reaction due to changes in only one part of the call. L and R call units were systematically

extracted from naturally produced LA and RA call unit combinations. We further made sure that all unfamiliar L and R call units came from different individuals by using recordings from a different group. Only R calls composed of double units were used. 'A' call units were from identified and habituated adult females of the focal group (A_G) or the neighbouring group (A_N). For each focal female, group or neighbour identities were pseudo-randomly attributed. This was done to avoid complete pair-matching between group members: if the call from female A was used as a stimulus for female B, then the call from female B was not selected to serve as stimulus for female A, to prevent any particular social relationship between two individuals to be over-represented. 'A' call units can be subdivided into full arches (Af subtype) or broken arches (Ab subtype) (Fig. 1). Females differ in how they make use of this feature, with some females mainly using 'Af' or 'Ab' subtypes (Candiotti et al., 2012a). When editing playback stimuli, we used a group-member's most typical A subtype which was then matched with the corresponding subtype for the neighbouring female stimulus.

Playback stimuli were created using Raven Pro 1.4 Software. Call exemplars were selected based on recording quality and call duration (in seconds: mean ± *SE*: L = 0.170 ± 0.012 s, R = 0.108 ± 0.002 s, A = 0.293 ± 0.014 s). We amplified stimuli when necessary to obtain a naturalistic intensity. Final tests of broadcast intensity were made in the Taï National Park to make sure that stimuli's intensity was homogeneous and appropriate according to the natural background noise.

Experimental protocol

Three observers followed the study group from 9:00 to 17:00 local time. Before the first experiment, we ran a habituation phase on several consecutive days during which the equipment was installed underneath the middle of the group in an open area so that it was fully

visible to the subjects. We repeated this until the subjects stopped giving alert calls and lost interest in the equipment. Before starting an experimental trial, we ensured that the group was not travelling or foraging 30 m or higher, that no neighbours were in the vicinity and that no male loud calls had been produced for at least 15 min. The experimenters then selected the subject and positioned the playback equipment at an elevation of 4 to 6 m above ground using a telescopic perch, either in periphery of the group (stimuli made from neighbouring female calls) or within the group. For within group trials, we kept the speaker about 5 m to 10 m away from the A call unit providing female. We did not wait for the subject to move to a specific position within the group and tested her where she was. Hence, playbacks of intra-group calls have been given from varied positions (more or less peripheral) in the group, without any obvious consequence. For each playback, CC continuously observed the subject, while FB and FG followed the call provider (in-group trials) and handled the equipment, respectively. Before initiating a trial, we ensured that (1) the subject was fully visible, (2) the call provider was 5 to 10 m away from the speaker, and (3) no call was given by any group member for at least 8 s.

Playback stimuli were broadcast from a Marantz PMD660 solid-state recorder connected to a Nagra DSM speaker/amplifier and a Bose 151 Environmental speaker that had been mounted to a telescopic perch. We recorded the behaviour of the subject for 30 s and the group's vocal behaviour for 60 s following each trial.

We never performed more than two trials per day and never for more than two days in a row. We ensured that we never broadcast two combined calls of the same category within the same day and we did not test the same individual in two consecutive experiments. Each day, we performed one to three "mock" experiments (even on days when no experiment was scheduled)

by executing the full experimental protocol, but no sound diffusion, to prevent subjects from anticipating a trial.

Dependent variables

During the 30 s post-playback period, we described the behaviour of the subject as the total duration (s) and frequency (i.e., the number of times a behaviour was observed) of its posture (i.e., sitting, standing or in vigilance posture), locomotion (i.e., immobile, walking, running or jumping) and direction of gaze (i.e., looks at the speaker, above, under, at a conspecific, at the observer and scans the environment). We also scored the latency in seconds for four behaviours: adopting a vigilance posture, sitting, walking and looking at the speaker. Overall, this resulted in 32 variables to describe each subject's behavioural response.

During the 1 min post-playback period, we also quantified the group's vocal activity using the following variables: the latency to give first call (any call type), the number of social calls (Coye, Ouattara, Zuberbühler, & Lemasson, 2015), the number of alert calls (Coye et al., 2015), the number of calls given during vocal exchanges (a sequence of any calls separated by less than 3 s of silence), the number of isolated calls (any call given more than 3 s before or after another call), as well as the number of vocal exchanges (involving any call type) and the average number of calls involved in a vocal exchange.

Statistical analysis

We expected the subjects' responses to differ in several subtle behavioural indicators simultaneously (notably locomotion, vocalizations and direction of gaze), suggesting that multivariate testing was most appropriate to deal with the potential co-variation of the variables. Any pair of variables with an R Pearson's correlation coefficient above 0.7 was

considered colinear in case of which we systematically deleted one member of the colinear pair (Dormann et al., 2013; Katz, 2011). Then, we used a Linear Discriminant Analysis as a preliminary guide for variables selection but did not use this method for further statistical analysis due to repeated measures present in our data (see Mundry & Sommer (2007) for details on LDA and discussion of the case of repeated measures). This first, exploratory, step led to the selection of a subset of seven biologically relevant variables susceptible to represent subjects' reaction (group's vocal behaviour, subject locomotion and gaze direction) across the experimental conditions. We used five quantitative variables: Number of isolated calls (given more than 3 seconds before or after another call), Latency to give first call (s), Time spent walking (s), Latency before locomotion (s), Duration of first look to the speaker (s), and two binary variables: Presence/absence of Look towards the observer, and Presence/absence of Visual scanning of the environment (Fig. 3).

We calculated Gower's dissimilarity index between samples in the dataset (daisy{cluster}, R statistical software, Maechler et al., 2015). This index "summarises" the difference between two samples into a measure of distance, based on the samples' values for each variable included in the analysis. Gower's distance is a common method which allows the use of various types of variables (binary, ordinal, nominal and quantitative variables) (Gower, 1971; Oksanen et al., 2007; Podani, 1999). The two binary variables were treated as symmetric variables and no standardisation of variables was applied.

To study the impact of the introductory unit (L or R units) and the impact of the affix (A units from a group-member or a neighbour), we performed two separate non-parametric MANOVAs (Adonis{vegan}, R statistical software, Oksanen et al., 2007) on the matrixes of Gower's dissimilarity index, giving the distance between trials in LA_G-RA_G and RA_G-RA_N conditions

respectively. Both NPMANOVAs were two-tailed, included the type of stimulus and the identity of the subject as factors and were conducted using free permutation of the distance matrixes, as suggested by Anderson (2001) and Gonzalez and Manly (1998) for small datasets.

NPMANOVA is a non-parametric multivariate method involving the calculation of an F-ratio on an index of distances between samples. The computation of a p-value, like any other permutational test, involves a comparison of the test value (i.e., the F-ratio) obtained on the original dataset (i.e., the distance matrix) with test values computed on random permutations of the same dataset. See Anderson (2001) for detailed explanation of the method and equations, as well as Adams and Anthony (1996) for a discussion of the use of permutational tests on behavioural data.

We completed the analysis with graphic representation of the results to describe the nature of the behavioural changes (Fig. 3). We computed effect size for each variable included in the multivariate testing. We used Cliff's delta for the quantitative (i.e., count and continuous) variables (cliff.delta{effsize}, R statistical software, (Torchiano, 2015) using the original formula proposed by (Cliff, 2014). And we used risk difference (riskdifference{fmsb}, R statistical software (Nakazawa, 2015) with a 95% confidence interval for the binary variables.

Ethical note

Ethics approval was given by the St Andrews' University Ethics Boards; the research protocol was authorised in Côte d'Ivoire, by the Minister of Scientific Research and the 'Office Ivoirien des Parcs et Réserves' (OIPR). This study does not raise major issues regarding animal welfare. Study groups have been habituated to human presence and followed on a regular basis since 1990 while the continued presence of researchers and field assistants has had a significant

impact on decreasing firearms-based poaching activities in the area. The habituation to the playback equipment was conducted smoothly. Moreover, the call types broadcast during the playbacks are naturally given at relatively high frequency: LA calls: 19.8 calls per hour, RA calls: 2.7 calls per hour (Candiotti et al. 2012a). Intergroup encounters, as simulated by playbacks of RA_N combinations (involving A calls from a neighbour), occur on average once every three days (McGraw et al., 2007 p59). No playback enhanced male alarm calling behaviour or triggered any sign of group panic or other abnormal behaviour.

RESULTS

Impact of the Introductory Unit on subjects' reaction:

When analysing the impact of the introductory unit, the NPMANOVA showed a significant impact of the type of stimulus ($F_{1,7}$= 3.37, P=0.043) and no significant effect of the subject's identity ($F_{7,7}$= 1.71, P=0.142). Graphic representation of the variables measured, combined with measures of effect size, show that test subjects expressed distinct behavioural patterns in the different experimental conditions (Fig. 3). Playbacks of LA_G ('positive' introduction, A from a group member) and RA_G ('negative' introduction, A from a group member) stimuli caused differences in locomotion, vocal behaviour and gaze direction (Fig. 3). Latency before locomotion appears shorter after playbacks of RA_G than LA_G (medium effect size: N= 16, *Cliff's delta*= -0.47), although we found no clear difference in the time spent walking (negligible effect size: N= 16, *Cliff's delta*= -0.125). The group gave more isolated calls (i.e., calls not part of a vocal exchange) in the RA_G than in the LA_G condition, with a medium effect size (N= 16, *Cliff's delta*= -0.47).The latency to give a first call was shorter and much less variable in the RA_G than in the LA_G condition although only a negligible effect was detected (N= 16, *Cliff's delta*= 0.125). Finally, the duration of the first look towards the speaker (N= 16,

Cliff's delta= -0.031, negligible effect) and the presence of looks towards the observer (*N*= 16, *RD*= -0.125, *P*= 0.285) did not change between LA_G and RA_G conditions (0% of the LA_G trials, 12.5% of the RA_G trials), but subjects scanned the environment more after the playback of the negative (i.e., RA_G) stimulus (37.5% of the trials) than after playbacks of LA_G (0% of the trials; *N*= 16, *RD*= 0.375, *P*= 0.028).

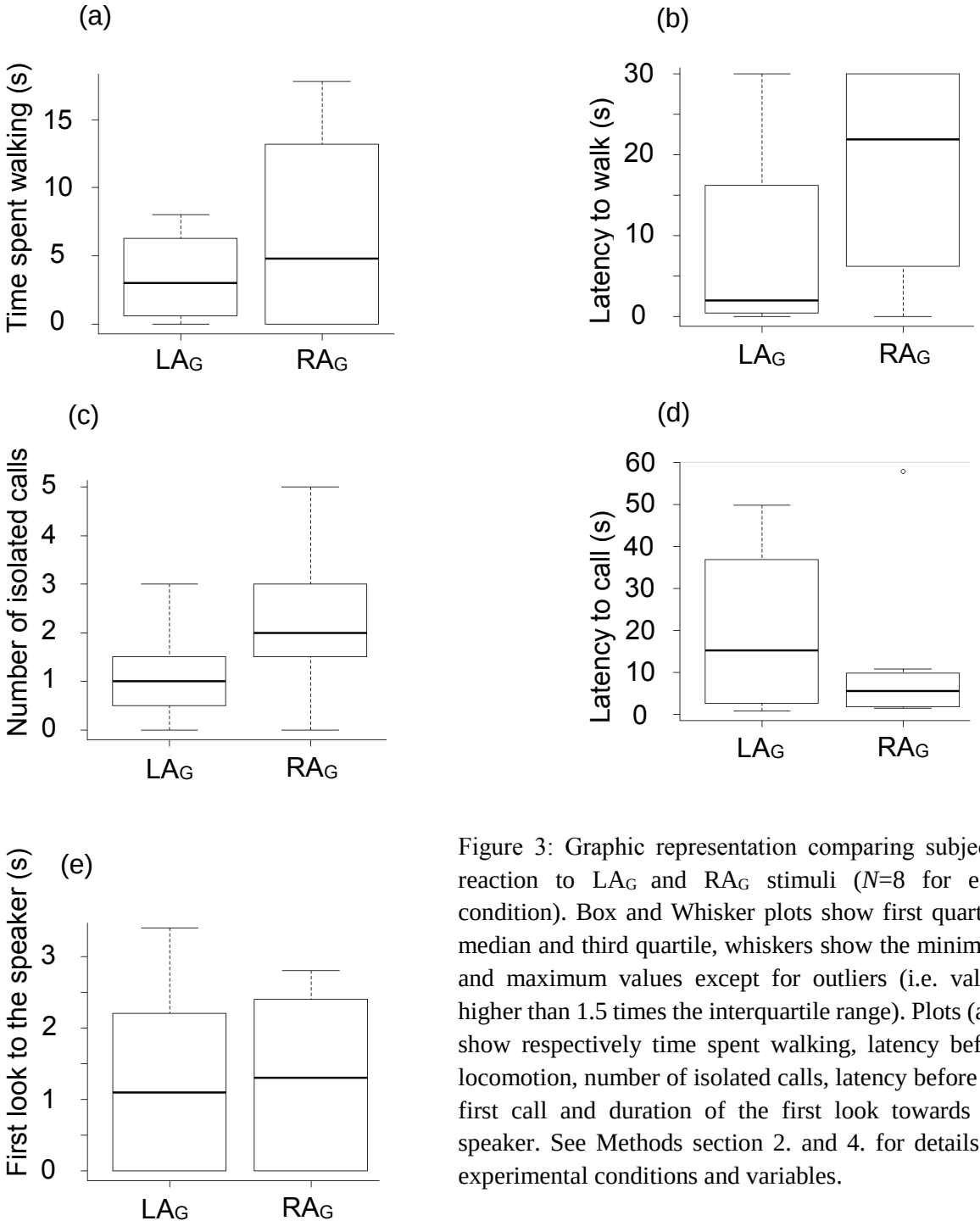


Figure 3: Graphic representation comparing subjects' reaction to LA_G and RA_G stimuli (*N*=8 for each condition). Box and Whisker plots show first quartile, median and third quartile, whiskers show the minimum and maximum values except for outliers (i.e. values higher than 1.5 times the interquartile range). Plots (a-e) show respectively time spent walking, latency before locomotion, number of isolated calls, latency before the first call and duration of the first look towards the speaker. See Methods section 2. and 4. for details on experimental conditions and variables.

Impact of the affix on subjects' reaction:

When analysing the impact of the affix, the NPMANOVA showed a significant impact of the type of stimulus involved ($F_{1,7}$= 4.29, *P*= 0.02) and no significant role of subject's identity ($F_{7,7}$= 1.66, *P*= 0.155). Graphic representation of the variables, combined with measures of effect size, show that test subjects expressed distinct behavioural patterns in the experimental conditions (Fig. 4): Comparison between responses to RA_G ('negative' introduction, A from group member) and RA_N ('negative' introduction, A from a neighbour) stimuli highlighted differences in locomotion, vocal behaviour and gaze direction but with a different pattern from the one found for the impact of the introductory unit (Fig. 4). Subjects spent less time walking (*N*= 16, *Cliff's delta*= 0.31, small effect size) and had a greater latency before locomotion (*N*= 16, *Cliff's delta*= -0.38, medium effect size) after playback of RA_N than RA_G stimuli. The results also suggest slight differences in group's vocal behaviour: groups gave fewer isolated calls (*N*= 16, *Cliff's delta*= 0.33) and displayed slightly greater and more variable latencies when giving the first calls (*N*= 16, *Cliff's delta*= -0.23) after playbacks of RA_N than RA_G stimuli. Finally, the pattern of gaze direction differed strongly between RA_G and RA_N stimuli: after playbacks of RA_N stimuli, subjects' first looks to the speaker were longer (*N*= 16, *Cliff's delta*= -0.73) with a large effect size. Subjects looked more at the observer (*N*= 16, *RD*= -0.375, *P*= 0.077) in the RA_N condition (50% of the RA_N trials vs 12.5% of the RA_G trials) but visual scanning of the environment did not seem to differ strongly between the playback of RA_G (37.5% of the trials) and RA_N (12.5% of the trials) stimuli (*N*= 16, *RD*= 0.25, *P*= 0.23).

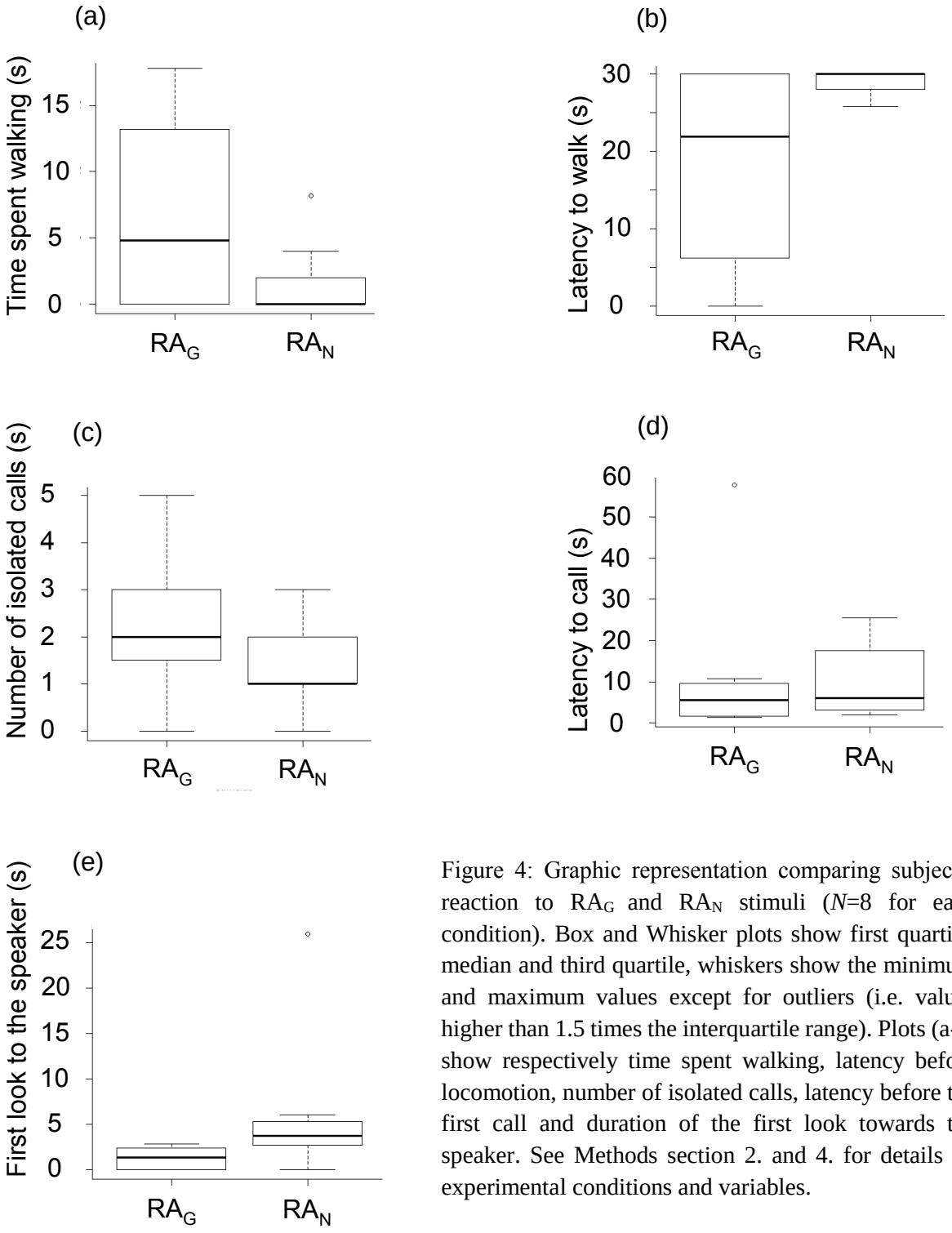


Figure 4: Graphic representation comparing subjects' reaction to RA_G and RA_N stimuli (N=8 for each condition). Box and Whisker plots show first quartile, median and third quartile, whiskers show the minimum and maximum values except for outliers (i.e. values higher than 1.5 times the interquartile range). Plots (a-e) show respectively time spent walking, latency before locomotion, number of isolated calls, latency before the first call and duration of the first look towards the speaker. See Methods section 2. and 4. for details on experimental conditions and variables.

DISCUSSION

In this study, we demonstrated experimentally that Diana monkeys responded differently to social calls composed of different morphological units in ways that suggested that at least two levels of information were conveyed. Morphological compounds consisted of L or R units, which related to different external events experienced by the caller (Candiotti et al., 2012a), and of A units, which related to caller identity. Response pattern suggested that recipients attended to these different levels of information conveyed by the call compounds. Specifically, our findings supported the idea that the initial morphemic unit of a combined call (L or R) encodes information about the social context experienced by the caller. R call units are typically associated with negative events, such as the detection of mild danger. Here, subjects responded with isolated social calls, prolonged latency before locomotion and scanning of the environment compared to L call units (typically associated with neutral and positive events) Overall, these results suggest that recipients associated the R and L call units with distinct socio-environmental contexts and adapted their behaviour accordingly.

The ability to reveal one's motivational states is a well-known function of animal communication (Briefer, 2012; Lemasson et al., 2012; Schehka & Zimmermann, 2009; Taylor & Reby, 2010), although it is often difficult to make a compelling argument about the exact nature of the underlying inner processes. Interestingly, the acoustically homologous call of Diana's monkey L unit in Campbell's monkeys increases in duration and frequency according to presumed differences in arousal (Lemasson et al., 2012). Here, we confirm the importance of this acoustic component to convey information about the emotional context, but we also show a different use in Diana monkey, whose social calls (L vs R) relate to the general valence of the external world as perceived by the caller. Importantly, L and R call units can be emitted singly or, more often, combined with A units into a compound call. More detailed contextual

analyses are required to determine which social situations are associated with single or combined calls. For example, it is possible that the distance between the caller and the receiver determines whether an A unit is affixed. Another possible explanation lies in variations in the degree of visibility in the habitat (Candiotti et al., 2012a, 2012b).

Call compounds that contained A units from a neighbouring individual ('RA_N') triggered a high decrease of locomotion, a slight decrease of vocal activity and an increased visual scanning towards the presumed caller compared to call compounds that contained A units from a group-member ('RA_G'). This pattern is similar to what has been in observed in other primates reacting to unexpected stimuli (Bergman, Beehner, Cheney, & Seyfarth, 2003; Briseño-Jaramillo, Estrada, & Lemasson, 2014; Zuberbühler & Wittig, 2011). These behavioural patterns suggest that both RA stimuli were perceived as urgent but that subjects based decisions on differences in the Affix.

Individual acoustic variations and auditory discrimination by receivers have been reported in many primate species (putty-nosed monkeys *Cercopithecus nictitans*: Price, Arnold, Zuberbühler, & Semple, 2009; marmosets *Callithrix jacchus*: Miller & Thomas, 2012; Olive baboons *Papio hamadryas anubis*: Lemasson, Palombit, & Jubin, 2008; Japanese macaques *Macaca fuscata*: Ceugniet & Izumi, 2003; squirrel monkey *Saimiri sciureus*: Kaplan, Winship-Ball, & Sim, 1978), suggesting that providing identity cues in primate calls is of considerable biological importance (Blumstein, Verneyre, & Daniel, 2004; Lemasson et al., 2007; Seyfarth et al., 2010; Seyfarth & Cheney, 2010).

This is likely so in this species in which vocal exchanges play an important role to ensure social cohesion and in which females differ in their vocal activity depending on their social integration within the group (Candiotti et al., 2015). In line with this, a previous study on Campbell's monkeys found that familiar calls (using homologous calls of Diana monkeys' LA)

elicited more affiliative calling and vocal responses than unfamiliar calls (Lemasson et al., 2005). Taken together, the responses given by the subjects to the different types of stimuli suggest that the first unit (i.e., L or R) allows the receiver to get information about the direct social and physical environment –probably by associative learning- while the identity conveyed by the second unit (A) may influence receiver's decision regarding the behaviour to adopt in line with their respective positions in the social network. For example, receivers may have different reactions depending on the identity of the caller when hearing an RA call which signals that a given individual has spotted something disturbing. But it seems premature to draw stronger conclusions about the relative importance of both types of information conveyed as here no playback of LA_N call was done. In future experiments, it would therefore be necessary to test subjects' reaction to L call units combined with A call units from neighbours as well as L call units combined with A calls from immature or more or less affiliated group members.

Our study has high external validity because the data are from spontaneous reactions of untrained and free-ranging animals living in their natural habitat. The results obtained here suggest that the main social calls given by the adult females are linear combinations of different morphological units that convey information about the social context and the identity of the caller. In a related study based on analysis tools from formal linguistics (Veselinovic et al., 2014), call sequences of wild adult females Diana monkeys were analysed which revealed non-random patterns in terms of the order and type of calls units that were merged. The authors concluded that calls consisting of combinations of call units functioned as single calls rather than rapid sequences of independent units (Veselinovic et al., 2014).

Nevertheless, this study remains only a first step towards understanding the use of complex calls and combinatorial abilities. Several technical and conceptual limitations must be acknowledged. Firstly each combined stimulus was created from call units taken from two distinct individuals and we do not know if the same reactions would be observed if we combined calls from the same caller. This choice was based on evidence in Campbell's monkey, a closely related species, that calls homologous to L and R calls in Diana monkeys (i.e., SH and RRC calls) relate to a much lesser extent to caller's identity than the arched structure homologous to Diana monkeys' A calls (i.e., *CH*) (Lemasson and Hausberger, 2011). Hence, if those data suggest that receivers discriminate caller's identity mostly from the arched part of the call, its actual importance in L and R calls remains to be tested in Diana monkeys. However, the fact that LA_G did not trigger any reaction showing that subjects were disturbed supports our hypothesis.

Moreover, in our experimental design, the L and R units of stimuli were taken from combined calls but A units were taken from calls emitted alone (i.e., not combined to another unit). The question remains whether the acoustic structure of A calls (when combined or not) differs slightly. But again, the fact that LA_G (socio-positive calls) did not trigger disturbed reactions in subjects suggests that this question may remain peripheral for the results obtained here. Testing this question could generate an interesting comparison with males Campbell's monkeys in which previous work found similar responses to natural Krak calls and artificial Krak calls created from Krak-oo calls (Coye et al., 2015).

An alternative solution to determine both the potential of the first unit (i.e., L or R) to signal caller's identity, and the influence of a possible variation in the structure of A calls' between combined and single calls would be to develop a playback experiment comparing sets of artificial stimuli. Notably a set of artificially combined calls created from single calls (i.e., L,

R and A calls combined in LA and RA complex calls) and a set of artificial 'single calls' taken from complex calls (i.e., breaking down LA and RA calls into L, R and A units), using either calls from a group-member or calls from a neighbour.

Interestingly, combinatorial abilities have been found in several animal species both at the call level and at the sequence level, in both males and females, and notably in species where males are more integrated socially (Bouchet et al., 2013; Bouchet, Laporte, Candiotti, & Lemasson, 2014; Bouchet et al., 2010; Coye et al., 2015; Lemasson, 2011; Ouattara, Lemasson, & Zuberbühler, 2009b). Although most studies based their conclusions on contextual and acoustic (non-experimental) analyses, they all suggest that combinatorial phenomena are an evolutionary adaptive response to an increased need for complex communication, which may be more widespread than initially thought. Whether the combinatorial abilities of non-human and human primates originated in an ancestral capacity or result from convergent evolution remains unclear and will require further comparative studies, notably to investigate phylogenetic and cognitive aspects of the evolution of combinatorial phenomena.

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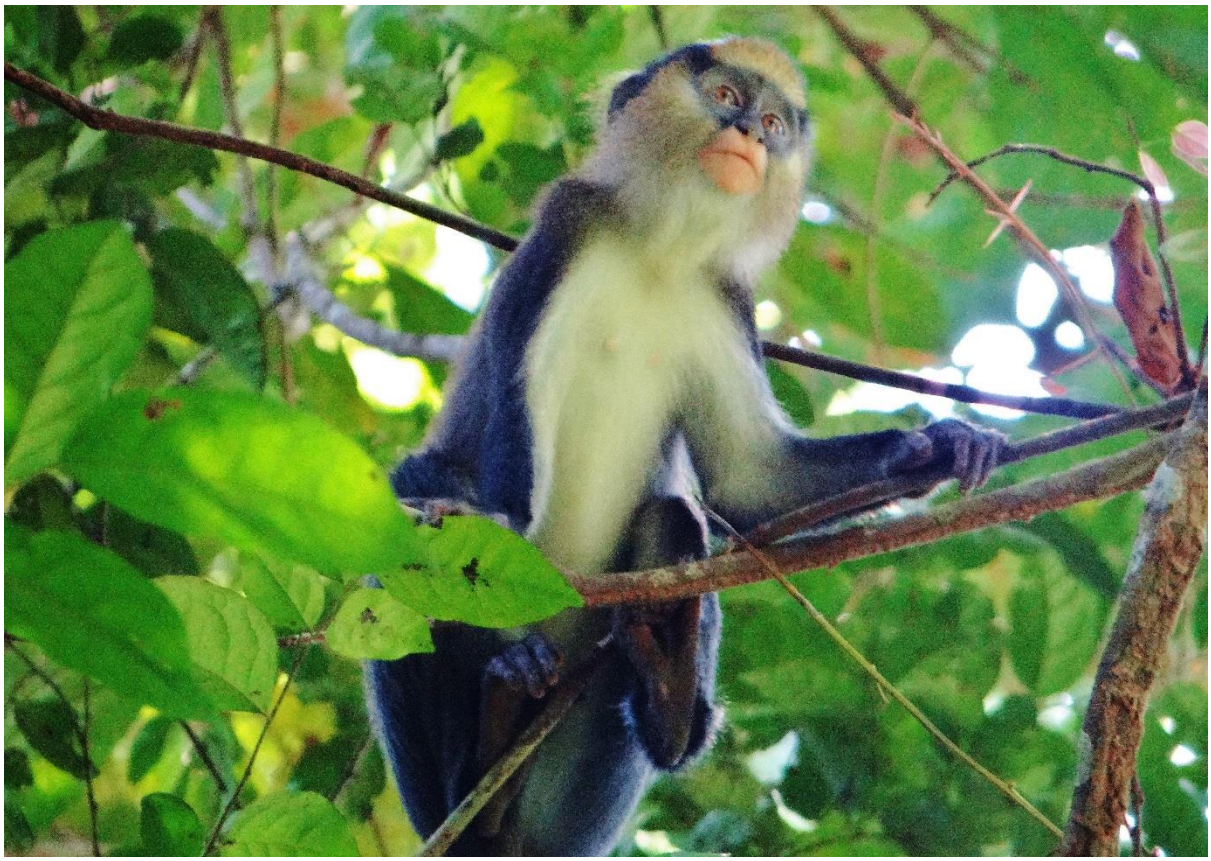
CHAPTER 5

COMPLEXITY OF FREE-RANGING CAMPBELL'S MONKEYS' (*CERCOPITHECUS CAMPBELLI*) CALLS IS DETERMINED BY SOCIOECOLOGICAL FACTORS



Summary of article 3

Question: Female Campbell's monkeys possess simple SH calls that can be given alone or combined with two distinct arched unit subtypes (*i.e.* full or broken) to create CHf and CHb combined calls in a flexible system resembling that of female Diana monkeys. Previous studies showed that SH, CHb and CHf relate gradually to caller's identity, with CHf calls being the most acoustically distinctive between callers and SH the least. However, the factors influencing the use of one call (sub)type over the others remained unknown. Hence this observational study aimed at answering two questions: **Are there social or other environmental factors explaining call use by female Campbell's monkeys? In particular, which factors drive the use of distinct call types (simple *vs* combined calls) and subtypes (*i.e.* involving a full or a broken arched structure)?**

Methods: We recorded, using focal sampling, the activity, strata use and vocal behaviour of ten adult females in two habituated groups of wild Campbell's monkeys over several months. In addition, we performed a scan sampling every thirty minutes to record distance between group members, group's position in the territory and association in polyspecific groups. The calls uttered by focal females have been classified independently by two experimenters. We included the four most frequent call (sub)types given by the females, in the analysis: RRA (alarm), SH (simple call), CHb (combined call subtype with a broken arch) and CHf (combined call subtype with a full arch). For each call (sub)type, we analysed both call rate (*i.e.* number of calls per minute of observation) and the proportion of total calls given it represented. We analysed this variables as a function of factors relating to the 'historical' context (*i.e.* subject average social and spatial integration within the group), and to the 'immediate' context (subject's last behaviour before calling, strata, group's position in the territory, associated species and whether the call was part of a vocal exchange or not).

Results: This study revealed four main findings. Firstly, call use varied with the "immediate" context but not with subject's "historical" integration within the group (*i.e.* average socio-spatial integration). Secondly, alarm and contact calls differed significantly in their context of emission, consistently with previous findings, this highlighted the relevance of the variables chosen in this analysis. Thirdly, simple and combined calls were associated with distinct immediate contexts: contrarily to simple calls, combined calls were given preferentially during vocal exchanges and after visual scanning of the environment by the caller. Finally, our results revealed a gradation in contact call use as a function of variables relating to the need to signal identity (*i.e.* visibility and

background noise) and predation risk (*e.g.* strata used and polyspecific association). Indeed, the most conspicuous and identity-rich calls (CHf calls) were used preferentially when predation risk was low but the need to signal identity was high. On the contrary, simple calls (less conspicuous but with a lesser potential to convey identity) were used in higher proportions when the need to remain cryptic was high but the need to signal identity was low. Finally, CHb calls, which likely represented a middle balance between identity and crypticity were the most common contact call.

Conclusion: This study shed light on the flexible and context-dependent use of contact calls in Campbell's monkeys. More importantly, it confirmed the social importance of combined calls and supports the hypothesis that social life likely influenced the evolution of combinatorial capacities in primates. Finally, the possible influence of a trade-off between social needs and anti-predator strategies on the structure and use of social calls in these guenons highlighted the difficulty to disentangle the influence of distinct evolutionary forces on the evolution of communication.

Manuscript in preparation

Complexity of free-ranging Campbell's monkeys' (*Cercopithecus campbelli*) calls is determined by socioecological factors

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ABSTRACT

Call combinations may allow animals to expand the communicative power of small repertoires with acoustically inflexible elements. Male Campbell's monkeys' alarm call system has revealed both combinatorial and referential features, but little is known about comparable effects of female calls. Adult females produce alarm calls and three distinct sub-types of social calls. Here, we evaluate the flexibility of these female utterances as a function of their potential to signal identity and the context experienced by the caller. We found that females merge units in calls that reveal different levels of identity and that their use of distinct call types is indicative of on-going behaviour and ecological factors. We discuss these finding in the light of possible selection pressures having favoured the evolution of combinatorial signalling and in relation to social skills.

Key-words: call combination, evolution of communication, contact calls, referential signalling, vocal signature, vocal flexibility

Chapter 5: Complexity of female Campbell's monkeys' calls and socioecological factors

INTRODUCTION

Living in group entails social interactions and this requires coordination between group members. Various communication systems have evolved in response to the various cooperative and competitive challenges of social living, as for instance engaging in joint activities such as travelling or defence against predators, or to optimise foraging in the presence of competitors (Gautier & Gautier, 1977; Lehmann, Korstjens, & Dunbar, 2007; Oda, 1996; Uster & Zuberbühler, 2001; see Bennett & Cuthill, 1994; Osorio & Vorobyev, 2008; Wyatt, 2003 and Liebal, Waller, Slocombe, & Burrows, 2013 for reviews of animals' and primates' different modalities of communication).

Predation and social life have been suggested to be two major forces driving the evolution of complexity of animal communication (McComb & Semple, 2005; Pollard & Blumstein, 2012; Stephan & Zuberbühler, 2008) and that could have led to the emergence of different call types and subtypes increasing repertoire size and diversity (Bouchet, Blois-Heulin, & Lemasson, 2013; Gustison, Roux, & Bergman, 2012; Knotkova, Veitl, Šimbera, Sedláček, & Burda, 2009; Le Roux, Cherry, & Manser, 2009). Diversification of calls can involve either the development of stereotyped acoustic variations derived from a general structure, or distinct combinatorial patterns of fixed sound units (Bouchet, Pellier, Blois-Heulin, & Lemasson, 2010; Coye, Zuberbühler, & Lemasson, 2016; Lemasson & Hausberger, 2011). Notably, predation might have enhanced the diversification of alarm calls (Hauser, 1996) to convey distinct levels of urgency or to signal the presence of predators attacking from different locations (Furrer & Manser, 2009; Manser, 2001; Pereira & Macedonia, 1991) and social life could have enhanced the diversification of signals that relate to caller's activity and identity (Bouchet et al., 2013; Manser et al., 2014).

Individually distinctive calls are widespread throughout the animal kingdom, and play a major role in regulating relationships within and between groups (Jansen, Cant, & Manser, 2012; Kondo & Watanabe, 2009; Le Roux et al., 2009; Palombit, 1992; Poole, Payne, Langbauer Jr, & Moss, 1988; Radford, 2004; Radford & Ridley, 2008). However, all call types and subtypes do not vary similarly as call variability and potential to encode caller's identity depends on its function (Bouchet, Blois-Heulin, Pellier, Zuberbühler, & Lemasson, 2012; Lemasson & Hausberger, 2011). Inter-individual variation of nonhuman primates' contact call types is generally greater than that of than alarm call types (Bouchet et al., 2013; Bouchet et al., 2012; Lemasson & Hausberger, 2011). Alarm call subtypes emitted in urgent contexts are more stereotyped and vary less among individuals than less urgent alarm call subtypes (Keenan, Lemasson, & Zuberbühler, 2013; Kuhn, 2014). We can hence expect gradation of the potential of contact call subtypes to encode identity depending on their context of use. Starlings (*Sturnus vulgaris*) present a comparable example. The repertoires of these songbirds include song types and subtypes that vary in their structure and potential to encode the social and individual identities of the emitter (Adret-Hausberger, 1989). Furthermore, song (sub)type varies with the immediate socio-sexual composition of the audience and the immediate vocal context (Adret-Hausberger, 1982; Henry & Hausberger, 2001).

Contrarily to species of birds with open-ended repertoires, primates have more fixed vocal repertoires and display limited flexibility and control over the fine acoustic structure of their vocal production (Hammerschmidt & Fischer, 2008). Recent studies suggest that these animals combine calls to overcome communication constrains due to their lack of acoustic control (Collier, Bickel, Schaik, Manser, & Townsend, 2014; Jansen et al., 2012; Lemasson, 2011). This hypothesis has been discussed in the light of evidence of male guenons' abilities to combine sounds (Coye, Ouattara, Zuberbühler, & Lemasson, 2015; Ouattara, Lemasson, & Zuberbühler, 2009b, 2009c; Zuberbühler, 2002).

Here, we investigated the contextual use and potential social function of several common types of free-ranging female Campbell's monkeys' (*Cercopithecus* campbelli) vocalisations, *i.e.* one alarm call type and three acoustic contact call subtypes (Lemasson & Hausberger, 2011). Campbell's monkeys are territorial arboreal guenons living in West African primary forests that often travel in association with other primate species. They form harem groups within which the single male and the adult females interact rarely (Candiotti et al., 2015). Their vocal behaviour presents a marked sexual dimorphism and adult males rarely produce calls and then only in response to external disturbances (Ouattara et al., 2009a). Males' 'morpho-syntactic' combinations have been well studied as they merge different sound units to form more or less combined alarm calls and combine alarm calls into context-dependent sequences (Ouattara et al., 2009b) (Coye et al., 2015; Alban Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010). Adult females are philopatric, form stable social bonds with other females and constitute the social core of a group (Candiotti et al., 2015). Females are relatively vocal, a possible response to the restricted visibility of their habitat (Brown, Gomez, & Waser, 1995; Marler, 1965; Waser & Brown, 1986).

Although female Campbell's monkeys can produce alarm calls, their most common call types are contact calls. These calls have combinatorial features and consist of three call (sub)types (Lemasson & Hausberger, 2011): SH, CHb and CHf. SH calls (Short Harmonic), that have low-pitched structures, can be uttered alone or combined with an arched frequency modulation to form the CH (Combined Harmonic) subtypes (Fig. 1). The CHb subtype combines the SH type with an incomplete ('broken') arch, whereas the CHf subtype combines the SH type with a complete ('full') arch (Fig. 1). A relationship exists between a call's potential to encode individual identity and that call's acoustic complexity. Specifically, alarm calls are acoustically simpler than contact calls and thus encode a caller's identity to a lower degree (Bouchet et al., 2013; Lemasson & Hausberger, 2011). Moreover, the most complex of the three contact call

(sub)types, CHf, encodes individual identity the most strongly and SH the least (Lemasson & Hausberger, 2011).

Therefore we investigated the relationships between the merging pattern of sound units and external events experienced by female callers and their interactions with differences in signalling individual identity. To address this, we analysed free-ranging adult females' vocalisations patterns in relation to several socio-ecological variables. As suggested previously (Ouattara, Zuberbühler, N'goran, Gombert, & Lemasson, 2009), we predicted that alarm calls and contact calls would be associated with distinct contexts (notably stressful situations). As contact calls typically function as facilitators of socio-spatial cohesion, we predicted that identity-rich subtypes would be used preferentially: (1) during vocal exchanges and by group members frequently observed grooming one another and in close proximity; (2) when a caller was obviously looking for a partner; (3) in noisy situations such as in poly-specific associations; (4) when individuals felt the urge for closer cohesion such as when they were near the periphery of their home-range where intergroup encounters are more likely; and (5) in situations when visibility is low such as in dense vegetation or in the low forest strata.

MATERIAL AND METHODS

Study site and subjects

Data were collected between August 2006 and February 2007 from observations of two groups of free-ranging Campbells' monkeys (*Cercopithecus campbelli*) in Taï National Park, Ivory Coast (5°50'N, 7°21'W). Both groups were fully habituated to human presence, and their home ranges are well known (Ouattara et al., 2009b). Each group included one adult male and respectively 7 and 3 individually known adult females and their offspring. Campbell's monkeys spend most of their time in association with other species of primates, notably Diana monkeys

(*Cercopithecus diana*), but also lesser spot-nosed monkeys (*Cercopithecus petaurista*), Sooty mangabeys (*Cercocebus atys*), Olive colobus (*Procolobus verus*), King colobus (*Colobus polykomos*), and red colobus (*Colobus badius*) (Buzzard & Eckardt, 2007; Mcgraw & Zuberbühler, 2008).

Data collection

One observer (KO) followed each group from 7:30am to 5:00pm on alternative days. Every 15 min, an adult female was selected randomly and her behaviour was scored as foraging, locomotion, social interactions or vigilance. Vocalisations and strata used were also recorded (See Table 1 for definitions). Scan samples were taken every thirty minutes to score the position of the group in the territory, the number and identity of associated species and, for each adult group member visible, its distance to and identity of its closest group member (Table 1). Vocalisations were recorded with a Sony TCD D100 DAT recorder, a Sennheiser ME88 directional microphone (for monkey calls) and a Lavallier microphone (for spoken comments). A total of 54 hours of observations and recording were collected, concerning ten adult females (mean ± ES: 5.4h±0.43 per individual).

Call classification

Calls were classified by audio-visual inspection ANA software (Richard, 1991). One experimenter (MA) labelled the call type (using a classification based on the vocal repertoire proposed by Lemasson & Hausberger 2011 for this species), of each vocalisation emitted by the focal subject and noted whether the call was or was not part of a call exchange. We define a vocal exchange as a sequence of vocalisations emitted by several individuals, each separated by less than one second (Lemasson, Gandon, & Hausberger, 2010). Four acoustic categories were defined: RRA Alarm calls, SH calls (Short Harmonic), CHb calls (Combined Harmonic

'Broken' arch), CHf calls (Combined Harmonic 'Full' arch) that are three subtypes of Campbell's monkey contact calls (Figure 1). SH calls are short, low-pitched with quavered structures. SH calls can be merged with an arched structure to form CHf calls (when the arch is complete, *i.e.* full) or CHb calls (when the arch is partial, *i.e.* broken).

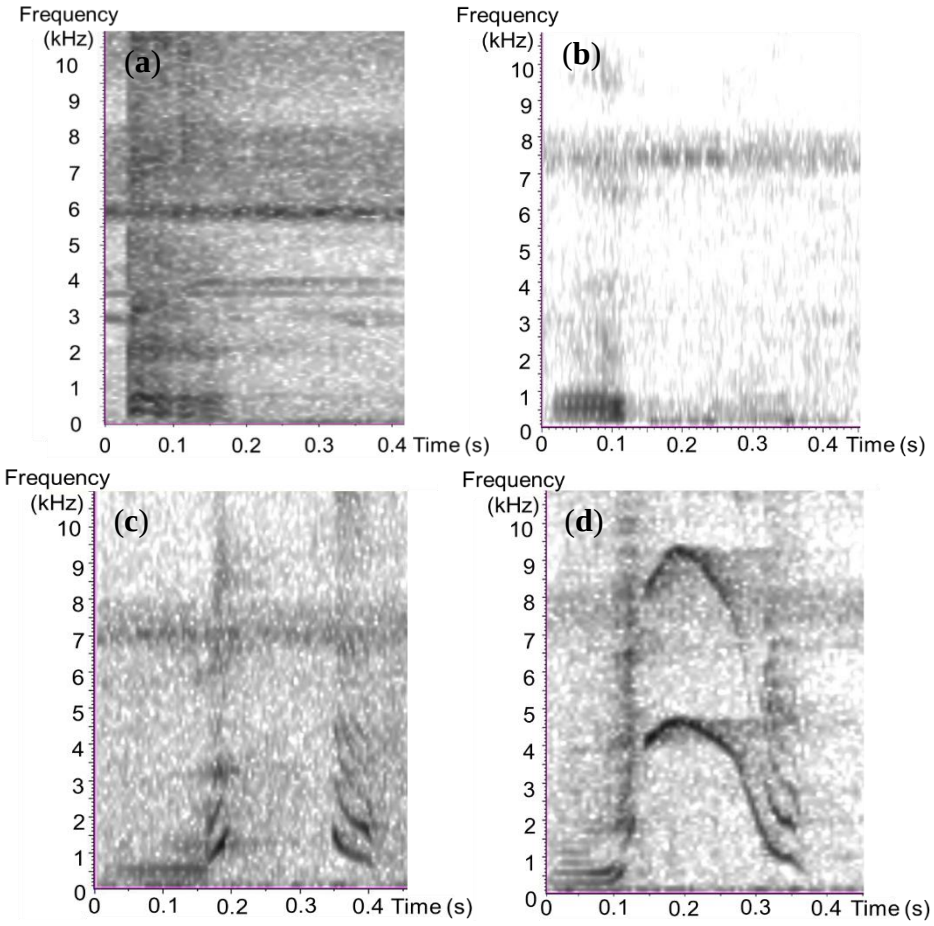

Figure 1: Spectrographic representation of female Campbell's monkeys' call (sub)types analysed: RRA: (a): alarm calls, (b): SH: low-pitched unit, (c): CHb: SH merged with a broken arch, and (d): CHf: SH merged with a full arch (see Lemasson & Hausberger 2011 for acoustic definitions).

Each vocalisation (N= 506) was then blindly labelled again by a second experimenter (CC) (using this time Raven Pro 1.4 software) to confirm the appropriateness of the call classification. Agreement between the two series of call (sub)type classified was 93.2%. A third researcher, the author of the abovementioned vocal repertoire (AL), gave advice concerning the appropriate classification for the calls without consensus.

Contextual analysis: variables measured and analyses

We analysed the influence of various socio-ecological factors on adult females' vocal behaviour (see Table 1 for definitions). As highlighted by Smith (1965), both the immediate context of a communication signal and the 'historical' context (*i.e.* the total of an individual's past experiences) in which it is emitted may be important. Hence, we analysed both 'historical' variables, related to the group's daily life, and the immediate contextual factors. To compensate differences among individual focal sampling data, we calculated individual call rates (*i.e.* the number of calls of a given type uttered during all focal samples of individual X, divided by the total observation time of individual X) and proportions of each type of call for each female (by dividing the number of this (sub)type call emitted by a female by the total number of calls emitted by that female). We used non-parametric statistical tests exclusively to perform the analyses.

i. "Historical" context: Subject's integration in its group

Subject's social integration in its group

To evaluate relationships between use of a call (sub)type and individual level of social integration in the group, we calculated separately time spent grooming (or being groomed by) the adult male, and any adult female in the group per minute of observation (*i.e.* divided by the total of focal observation time of the group) for each adult female. We performed a Spearman correlation test between call rate of each (sub)type and time spent grooming another adult in the group.

Subject's spatial integration in the group

To evaluate the impact of a subject's spatial integration in the group on call rate, we calculated the average distance of each individual to its closest neighbour by averaging the distances

measured (every half-hour during scan sampling) between the subject and its closest conspecific. We performed Spearman correlation tests between the rates of each call type and subject's average distance to its closest neighbour (from now DCN).

ii. 'Immediate' context

We examined the context of calls in a closer time frame (from now immediate context) using ecological and behavioural variables (from now, termed factors, to prevent confusion with the dependent variables). For this analysis, we used systematically both call rate and proportions of calls (*i.e.* dependent variables) whenever possible. These two methods for quantifying call use are complementary and susceptible to highlight different kinds of variations of call use.

Ecological context

We chose three ecologically relevant factors to evaluate the impact of the immediate ecological context on call use: density of associated primate species, the position of the group in its territory and subject's strata.

To estimate differences in call rates as a function of these three factors relating to the ecological context, we used either Wilcoxon rank sum tests or Friedman ANOVA depending on the number of categories of the factor (*i.e.* two levels: Wilcoxon test, more than two level: Friedman ANOVA, see Table 1 for information about the levels of each factor). When significant, Friedman ANOVAs were followed by pairwise Wilcoxon tests with False Discovery Rate correction. A continuity correction was applied to Wilcoxon tests when necessary. We performed this analysis for four of the five aforementioned variables because an unbalanced observational design prevented the use of a Friedman test on subject's strata (most subjects were observed in only three of the four strata). Hence, to assess a link between

call rate and caller's strata, we calculated a Spearman correlation between subject's strata when calling and call rate for each call type separately.

We analysed the proportion of each call (sub)type using binomial Generalized Linear Mixed Models (from now, GLMMs) with a logit link. The proportion of RRA calls was calculated over the total number all calls given (*i.e.* RRA + contact calls), but the proportion of each contact call subtype (SH, CHb and CHf) was calculated over the total number of contact calls given (*i.e.* SH+CHb+CHf calls) for a more precise discrimination. The model included systematically the contextual factor as the only fixed factor and subject's identity as a random factor (glmer() function, {lme4} R package). We computed post-hoc tests when necessary using least-squares means analysis (lsmeans() function, {lsmeans} R package).

Behavioural context

To qualify the immediate behavioural context of calls we analysed both the immediate vocal and non-vocal contexts. To determine whether the use of call types differed depending on the immediate vocal context, we tested whether each call (sub)types was emitted more alone (*i.e.* not during an exchange) or during an exchange (*i.e.* uttered within one seconds after another call). To this end, we compared the rates of calls emitted in isolation and during vocal exchanges for each call type using Wilcoxon tests with continuity correction. We compared the proportions of isolated and exchanged calls for each call type using a binomial GLMM (link: logit) including the vocal context (*i.e.* isolated or exchanged) as a fixed factor and subject's identity as a random factor (glmer() function, {lme4} R package).

The immediate non-vocal context was assessed by subject's last behaviour before calling, for which we used three main behavioural categories: Locomotion, Feeding and Observation of the environment (see Table 1 for definitions). To evaluate differences in call rates in relation

to the behaviour preceding a call, we used Friedman ANOVA followed by pairwise Wilcoxon tests with False Discovery Rate (FDR) correction. We analysed the proportion of each call (sub)type using binomial GLMMs (link: logit). The proportion of RRA calls was calculated over the total number all calls given (*i.e.* RRA + contact calls), but the proportions of each contact call subtype (SH, CHb and CHf) was calculated over the total number of contact calls (*i.e.* SH+CHb+CHf calls). The model included the behaviour preceding calling as a fixed factor and subject's identity as a random factor (glmer() function, {lme4} R package). We computed post-hoc tests when necessary using the least-squares means analysis (lsmeans() function {lsmeans} R package).

Table 1: Definition of the contextual variables used for the study. DCN stands for 'Distance to the Closest Neighbour'.

Analysis	Variable	Sampling method	Categories	Description	Behavioural units
'Historical' social integration	Grooming	Focal	With male	Time spent grooming the adult male, per minute of observation	NA
			With female	Time spent grooming an adult female, per minute of observation	
	Call exchanged	Focal	Exchanged	Call given within 1s from a call of a conspecific	
			Isolated	Call given more than 1s away from a call of a conspecific	
'Historical' spatial integration	DCN	Scan	Distance (m)	Distance to the closest conspecific (m)	
Immediate environmental context	Associated species	Scan	Low density	No or only one other primate group within 50 m. When another primate species was present, it was always a cryptic species, either in a smaller group (*C. Verus)* or with smaller individuals (*C. Petaurista*)	
			High density	Two associated species or more under 50m from the group	
	Group's position in the territory	Scan	Centre	More than 100 m from the border of the territory (Ouattara et al., 2009b)	
			Periphery	Under 100 m from the border of the territory (Ouattara et al., 2009b)	
	Strata (McGraw, 1998)	Focal	Strata 0	On the ground	
			Strata 1	0 - 5 meters from the ground	
			Strata 2	5 - 20 m high	
			Strata 3	20 - 40 m high	
Immediate behavioural context	Behaviour preceding the call	Focal	Socio-positive interactions	Affiliative interactions between the focal subject and a group member	Following x, going toward x, sitting or standing under an arm length from x, reaching x with hand, presenting a body part to x (grooming request), grooming x
			Socio-negative interactions	Agonistic interactions between the focal subject and a group member	Running away from x, going away from x, threatening x, fighting with x, biting x, pushing x
			Important locomotion	Potentially stressful locomotor activity	Going to the ground, climbing up or down (strata changes), jumping
			Feeding	Eat	The animal puts a food item in the mouth
			Observation	Observation of the environment	Scanning the ground, looking above and under, scanning the environment in vigilance posture

RESULTS

i. 'Historical context': Subjects' integration in their group

Subjects' social integration in their group

The level of social integration of an individual, assessed through grooming frequencies with group members, was not correlated significantly with preferential use of any call (sub)type. No correlations between call rates (of any call type or subtype) and the time each subject spent grooming the adult male or adult females could be evidenced (Spearman correlation tests: N= 10, Df= 8, FDR correction for four multiple correlations; Adult male: RRA calls: S= 249.60, p= 0.13, rho= -0.51 ; SH: S= 162.94, p= 0.97, rho= 0.02; CHb: S= 217.62, p= 0.37, rho= -0.32; CHf: S= 142.30, p= 0.71, rho= 0.14; Adult females: RRA calls: S= 186, p= 0.74, rho= -0.13; SH: S= 98, p= 0.25, rho= 0.41; CHb: S= 136, p= 0.63, rho= 0.18; CHf: S= 114, p= 0.39, rho= 0.31).

Subjects' spatial integration in their group

The average level of spatial integration of an individual in their group was not correlated with preferential use of any call (sub)type. No correlations between the average distance to the closest neighbour and call rates could be evidenced (Spearman correlation, p-values adjusted for multiple comparison using FDR method: N= 10, Df= 8, RRA calls: S= 232, p= 0.407, rho= -0.41; SH: S= 110, p= 0.407, rho= 0.33; CHb: S= 116, p= 0.407, rho= 0.30; CHf: S= 116, p= 0.407, rho= 0.30).

ii. "Immediate" context

Ecological context

Density of associated primate species

The density of surrounding (associated) primate species at the time of calling influenced call type and subtype emitted. Analyses of call rates and call proportions evidenced this effect.

RRA call rates and CHf call rates were significantly higher when the density of associated species was high than when it was low. However, the density of associated species did not influence the rate of SH calls and CHb calls significantly (Wilcoxon rank sum test, N= 10 individuals, RRA calls: W= 10, p= 0.0006; SH calls: W= 35, p= 0.27; CHb calls: W= 32.5, p= 0.50; CHf calls: W= 18, p= 0.02).

The proportion of SH calls was significantly higher when the density of associated species was low than when it was high (Binomial GLMM, Df= 3, RRA calls: Chisq= 11764875, p<0.0001; SH calls: Chisq= 9.41, p= 0.0022). Density of associated species did not influence significantly the proportions of RRA calls, CHb and CHf calls (Binomial GLMM, Df= 3, RRA calls: Chisq= 0, p= 0.9972; CHb calls: Chisq= 0.0125, p= 0.91; CHf calls: Chisq= 2.19, p= 0.14).

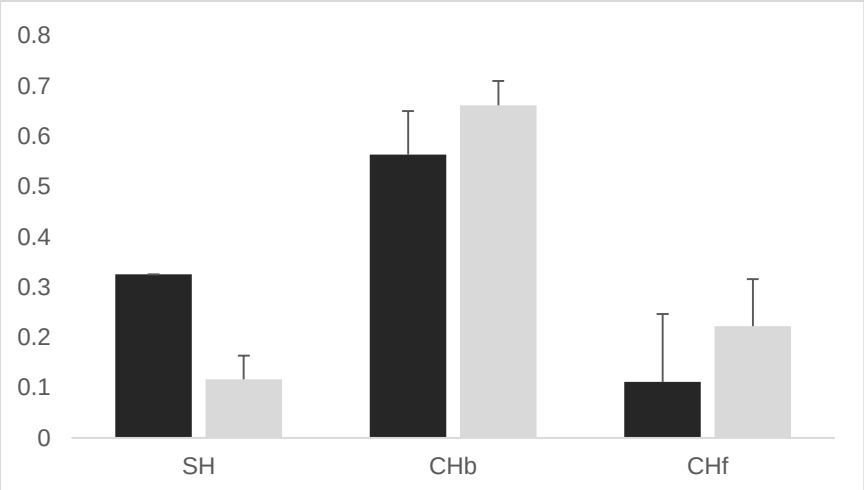

Figure 2: Mean proportion of total social calls given represented by SH, CHb and CHf calls when the density of associated species was low (dark bars) or high (grey bars). Error bars show the standard error of the mean. Please note that, as the proportions were calculated over total calls given in each context, the sum of bars for a given call type does not reach 100% but the sum of bars of the same colour does. See Table 1 and Methods section 4.2 for details of the analysis.

Group's position in their territory

The group's position in the territory at the time of calling influenced the contact call subtype emitted preferentially as call proportions varied significantly with position although call rates did not differ significantly between centre and periphery of the territory (Wilcoxon rank sum

test, N= 10 individuals, RRA calls: V= 28, p= 0.18; SH calls: V= 37, p= 0.37; CHb calls: V= 24, p= 0.91; CHf calls: V= 14, p= 0.34).

Significantly higher proportions of CHf calls were emitted at the periphery than in the centre of the territory, but the proportions of the other call (sub)types did not differ significantly with position in the territory (Binomial GLMM, N= 10, Df= 1, RRA calls: Chi^2= 1.57, p= 0.21; SH calls: Chisq= 0.0025, p= 0.96; CHb calls: Chisq= 0.64, p= 0.43; CHf calls: Chisq= 4.74, p= 0.029).

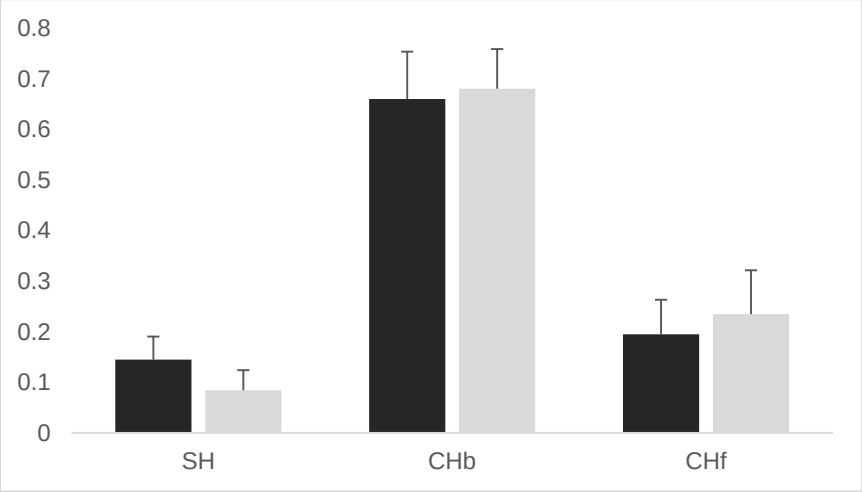

Figure 3: Mean proportion of total social calls given represented by SH, CHb and CHf calls in the centre of the group's territory (dark bars) or at the periphery (grey bars). Error bars show the standard error of the mean. See Table 1 and Methods section 4.2 for details of the analysis.

Callers' strata

Strata occupied by subjects influenced call use, and strata and both rates and proportions of several call (sub)types were correlated (Fig. 3).

RRA and CHf calls rate were correlated with subject's strata at the time of calling (Spearman correlation, N= 10 individuals, RRA calls: S= 7670.23, p= 0.0015, rho= -0.55; CHf calls: S= 7547.13, rho= -0.52, p= 0.0026). Subjects emitted RRA and CHf calls at higher rates when they were in the lower strata (mostly strata zero – on the ground) than in the higher strata. No

significant correlations could be evidenced for SH and CHb call rates (Spearman correlation, N= 10 individuals, SH calls: S= 6493.2, p= 0.09, rho= -0.3091; CHb calls: S= 5342.5, p= 0.68, rho= -0.08) and subject's strata.

The proportions of CHf calls were significantly higher when subjects were in strata 0 (*i.e.* on the ground) than in strata 1 (Binomial GLMM, Df= 3, Chisq= 10.45, p= 0.015; least square means: S0-S1: z= 3.12, p= 0.01; S0-S2: z= 2.31, p= 0.09; S0-S3: z= 2.01, p= 0.18; the other comparisons: z<1 and p-values >0.2). Interestingly, the proportions of CHb calls, on the contrary, were significantly higher in strata 3 than in strata 0 (Binomial GLMM, Df= 3, Chisq= 9.65, p= 0.022. least square mean: S0-S1: z= -2.23, p= 0.11; S0-S2: z= -2.07, p= 0.16; S0-S3: z= -3.05, p= 0.01; the other comparisons: z<1 and p-values >0.2). Finally, the proportions of RRA calls and SH calls did not differ significantly between strata (Binomial GLMM, Df= 3, RRA calls: Chisq= 0.64, p= 0.89; SH calls: Chisq= 1.08, Df= 3, p= 0.78).

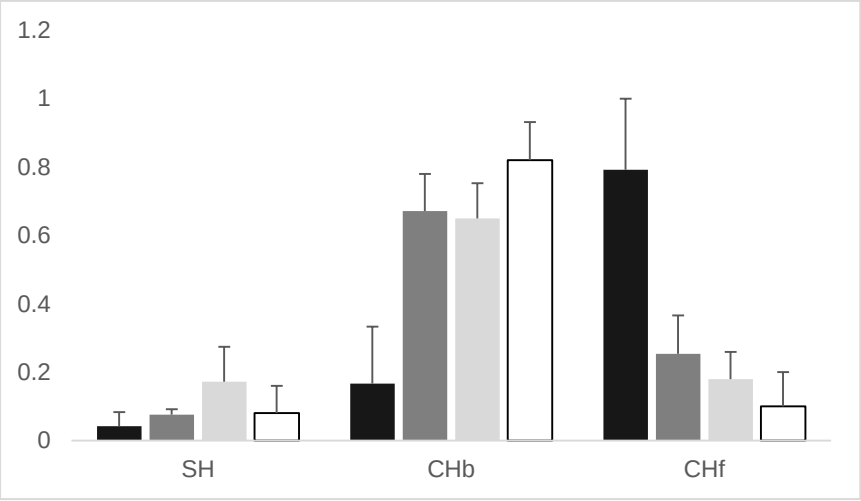

Figure 4: Mean proportion of total social calls given represented by SH, CHb and CHf calls at each strata (stratum zero: black bars, stratum 1: dark grey bars, stratum 2: light grey bars, stratum 3: white bars). Error bars show the standard error of the mean. See Table 1 for definitions and Methods section 4.2 for details of the analysis.

Behavioural context

Propensity to exchange vocally with group-members

The levels of vocal exchange varied with call type and subtype (Fig. 2). The rates of RRA were significantly higher for isolated than exchanged calls (Mann-Whitney, N= 10, RRA: V= 45, p= 0.009), but the rates for the three contact call (sub)types emitted alone or during exchanges did not differ significantly (Mann-Whitney, N= 10, SH: V= 18, p= 1; CHb: V= 11, p= 0.19; CHf: V= 5, p= 0.08).

The proportions of RRA calls were significantly higher when uttered in isolation than when involved in a vocal exchange (Binomial GLMM, Df= 1, Chisq= 43.04, p<0.0001). Similar proportions of SH contact calls were uttered alone and during exchanges, but the proportions of CHb and CHf calls were significantly higher when emitted during an exchange than alone (Binomial GLMM, Df= 1, SH: Chisq= 1.56, p= 0.21; CHb: Chisq= 3.99, p= 0.046; CHf: Chisq= 18.36, p<0.0001).

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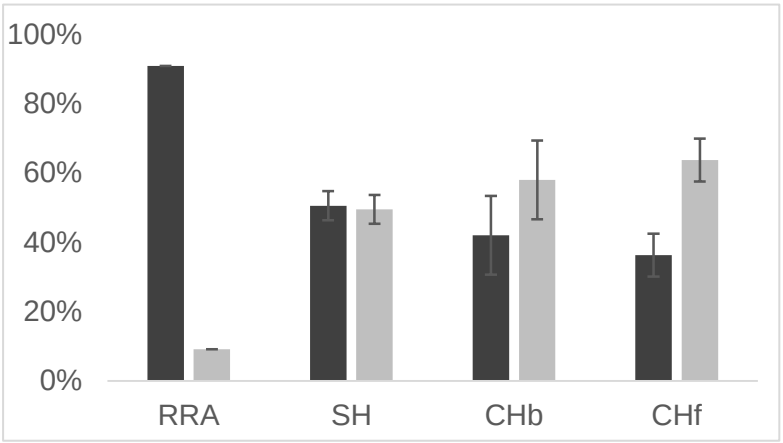


Figure 5: Average proportions of each call (sub)type emitted alone (dark grey) or during exchanges (light gray), error bars show the standard error of the mean. See Table 1 for definitions and Methods section 4.1 for details on the analysis.

Behaviour preceding a call

A subject's behaviour immediately before calling related to the call (sub)type preferentially used. Rates of calling differed significantly depending on the behaviour preceding the call for every call type and subtype tested, with similar results for all call categories (Friedman Anova,

N= 10, Df= 2, RRA calls: Chisq= 9.21, p= 0.01; SH calls: Chisq= 15.74, p= 0.00038; CHb calls: Chisq= 14.82, p= 0.0006; CHf calls: Chisq= 9.21, p= 0.01). Indeed, post-hoc tests showed that the rates of all (sub)types calls emitted after observation were significantly higher than after locomotion or foraging (Pairwise Wilcoxon tests with false discovery rate correction, N= 10 individuals, Comparison Observation vs Locomotion: RRA: p= 0.034, SH: p= 0.014, CHb: p= 0.014, CHf: p= 0.034; Observation vs Foraging: RRA: p= 0.034, SH: p= 0.014, CHb: p= 0.014, CHf: p= 0.034; Locomotion vs Foraging: RRA: p= 0.59, SH: p= 0.42, CHb: p= 0.11, CHf: p= 0.79).

However, the analysis of call proportions revealed distinct patterns for several call types (Fig. 4). First, the proportions of RRA calls emitted after locomotion were significantly higher than after observation, and the proportions of RRA calls emitted after these two behaviours were also significantly higher than after foraging (Binomial GLMM, Df= 2, Chisq= 48973, p<0.0001; least square means: L vs O: z= -119; L vs F: z= -186; O vs F: z= 46; p<0.0001 for the three tests). Distinct behavioural patterns were associated with contact call types. Proportions of SH calls were significantly higher after foraging than after either observation or locomotion but did not differ significantly between these two behaviours (Binomial GLMM, Df= 2, Chisq= 59.41, p<0.0001; least square mean: F vs O: z= 7.61, p<0.0001; F vs L: z= 3.64, p= 0.0008; O vs L: z= 2.09, p= 0.09). On the contrary, proportions of CHb calls were significantly lower after foraging than after observation or locomotion but again did not differ between these two categories (Binomial GLMM, Df= 2, Chisq= 28.01, p<0.0001; least square mean: F vs O: z= -5.29, p>0.0001; F vs L: z= -2.55, p= 0.029; O vs L: z= -1.38, p= 0.35). Proportions of CHf calls were significantly higher after observation than after foraging but did not differ between observation and locomotion or between locomotion and foraging (Binomial GLMM, Df= 2, Chisq= 6.14, p= 0.046; least square mean: F vs O: z= -2.47, p= 0.036; F vs L: z= -1.75, p= 0.19; O vs L: z= -0.21, p= 0.98).

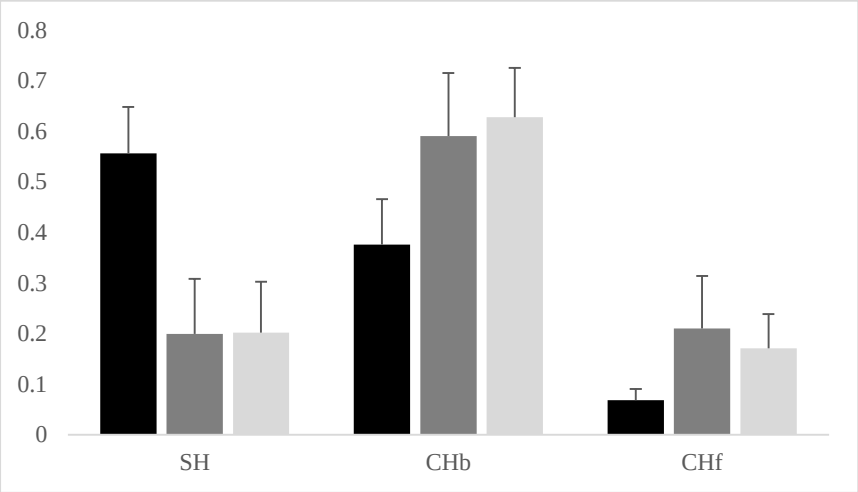


Figure 6: Mean proportion of total contact calls given represented by SH, CHb and CHf calls immediately after foraging (black bars), locomotion (dark grey bars) and observation (light grey bars). Error bars show the standard error of the mean. See Table 1 for definitions and Methods section 4.2 for details on the analysis.

DISCUSSION

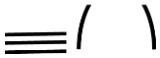
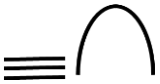
Our study aimed to understand the contextual and socio-ecological factors influencing the use of two different call types (alarm and contact calls) and the flexible use of three contact call subtypes (SH, CHb and CHf), varying gradually in their complexity and in their potential for identity coding in two groups of free-ranging Campbell's monkeys. We showed that sound merging was optional but not random as contact call complexity was context-dependent.

Immediate vs 'historical' contexts

Our results suggested that the call (sub)type used depended mostly on the immediate calling context more than on callers' social experience. Both variables reflecting an individual's social and spatial integration in her group (*i.e.* time spent grooming others and average distance to her closest neighbour) failed to evidence any significant correlation with calling preferences. This confirmed the flexible use of sound merging on a short time scale by female Campbell's monkeys. Although call subtype use did not vary with historical context here, a previous study

demonstrated that the fine acoustic structure of CHf (complex, full-arched calls) varied with individuals' social relationships as CHf acoustic variants (identified by a particular shape of the arched frequency modulation) were shared by affiliated partners (Lemasson & Hausberger, 2004; Lemasson, Ouattara, Petit, & Zuberbühler, 2011).

Table 2: Main results concerning the immediate contextual factors

		Alarm calls	Contact calls		
				Arch addition **Arch completeness**	
Type of context	Factor	RRA 	SH 	CHb 	CHf 
Ecological context	Density of associated species	High	Low	-	High
	Group's position in the Territory	-	-	-	Periphery
	Caller's strata	Low	-	High	Low
Behavioural context	Pattern of vocal production	Isolated	-	Exchanged	Exchanged
	Behaviour preceding the call	Locomotion	Foraging	Observation	Observation

Alarm vs contact calls

Our analysis of the immediate context of emission clearly separated emission of alarm calls from that of contact calls (Table 2). Conversely to contact calls, alarm calls were typically emitted in isolation, confirming that they functioned primarily to signal danger. The danger signalled can have been either detected (presence of a predator) or perceived (stress or discomfort experienced). Supporting this hypothesis, our data showed that alarm call frequencies increased mainly in potentially stressful situations (Table 2): when several other species were nearby (this may be true in particular for Campbell's monkey groups, as this

species is considered to be "subordinate" in the poly-specific community; Buzzard, 2006a; McGraw, Zuberbühler, & Noë, 2007); when the caller was travelling (*i.e.* increased probabilities to perceive unspotted disturbances), and notably when moving near or on the ground (a potentially stressful situation for arboreal animals). All these results confirmed the relevance of the contextual and behavioural parameters chosen for our analyses and highlighted the distinct use and possible functions of this species' alarm and contact calls (Ouattara et al., 2009). More interestingly, the different contact call subtypes were not emitted at similar frequencies or under similar conditions.

Simple vs Combined calls: optional arch addition

Our results revealed several contextual factors that opposed simple to combined calls. Conversely to simple calls, combined subtypes (CH calls) were used preferentially during vocal exchanges (Table 2). This confirmed the important role played by the arch during vocal exchanges among group members, probably as a consequence of the potential of this structure to encode identity. Campbell's monkeys' vocal exchanges play a major role in the regulation of both social and spatial cohesion and caller's identity influences strongly receivers' responses (Lemasson, Gandon, et al., 2010; Lemasson, Hausberger, & Zuberbühler, 2005).

In addition, the analysis of the behaviour preceding calling reinforced the dichotomy between (non-combined) SH calls and (combined) CH calls: SH calls were associated with foraging while CHb and CHf calls were associated with observation. This contextual opposition was consistent with the acoustic structures of the calls. Simple calls (SH), which relate less to caller's identity, were associated with foraging. Foraging is an individual activity typically associated with short inter-individual distances (due to dense food patches; Buzzard, 2006a, 2006b), probably reducing the need and the motivation for vocal contact and social interaction. On the contrary, the two combined structures (CH), which relate more strongly to caller's

identity, were used after visually scanning of the habitat and conspecifics, probably as a result of enhanced motivation to engage in social activities.

SH vs CHb vs CHf calls: arch addition and completeness, an "identiy-crypsis" trade off

We propose that the differential use of the three (sub)types could depend on a trade-off between the need to signal caller's identity on the one hand and the need to remain cryptic and avoid predation on the other hand. In addition to the gradation of identity-encoding between SH, CHb and CHf calls, another gradation exists between these three call subtypes concerning their frequency range and intensity: the maximum frequency and intensity of calls increase gradually from SH, to CHb and to CHf (respectively 846 Hz, 1800-2000 Hz and around 3558 Hz on average; Lemasson & Hausberger, 2011). SH calls, as the most cryptic contact call, were used in higher proportions or at higher rates when predation risk was the highest, *i.e.* in the lower strata, when alone or associated only with a cryptic species (Boinski, Treves, & Chapman, 2000; Mcgraw & Zuberbühler, 2008). In this case, the need to signal caller's identity might be weaker as Campbell's monkeys stay relatively stationary when they are not associated with more than one other monkey species (Buzzard, 2004). On the contrary, CHf calls represent the 'identity-rich' extreme of the 'identity vs crypsis' trade-off. These calls were associated with contexts in which the need for identity cues was the greatest: when several species were associated (many animals moving and a possible confusion effect; Mathevon, Charrier, & Jouventin, 2003) on the border of their territory (increased need for group cohesion and potential competition with neighbouring groups; (Ouattara et al., 2009b) and in the canopy strata where visibility is poor (Candiotti, Zuberbühler, & Lemasson, 2012b). The increase of both RRA and CHf call rates when the density of associated primates was high is consistent with the suggestion that polyspecific associations reduce predation pressure (thus allowing the use of less cryptic calls) but increase competition between species (Buzzard, 2006b; Mcgraw

& Zuberbühler, 2008). CHb calls probably represent the balance between identity and crypsis. Consistently with this, they were Campbell's monkeys' most common contact calls and did not seem associated strongly with any particular context.

The association of the gradual increase of the risk of being detected with more complete structures is supported by the characteristics of the hearing capacities of Campbell's monkeys' main predators (*i.e.* leopards (*Panthera pardus*), crowned hawk eagle (*Stephanoaetus coronatus*) and chimpanzees (*Pan troglodytes*); McGraw et al., 2007). All these predators detect low frequency sounds (*i.e.* < 1 kHz) less efficiently than higher frequency sounds (*i.e.* around 4kHz) (Heffner, 2004; Heffner & Heffner, 1985; Huang, Rosowski, & Peake, 2000; Yamazaki, Yamada, Murofushi, Momose, & Okanoya, 2004). Thus Campbell's monkeys' predators are able to detect the arched structures of CH calls, and especially the peak of the arch of CHf calls, at lower sound intensities than SH calls. Authors have described cases of 'hiding' from their predators (*i.e.* 'acoustic avoidance'; Ruxton, 2009) or using acoustic signals that limit detection by predators ('acoustic crypsis') by animals of various species from marine mammals (Morisaka & Connor, 2007) to birds (Klump, Kretzschmar, & Curio, 1986) and insects (Ruxton, 2009) that constitute important mechanisms of defence against predation. Here the system described revealed an additional layer of complexity as Campbell's monkeys' call use reflected both acoustic crypsis to avoid predation and a trade-off between avoiding predation and the need to signal identity.

Towards a more widespread use of context-dependent sound merging

Several well-known examples of call combination given in alarm contexts have been described (Arnold, Pohlner, & Zuberbühler, 2008; Clarke, Reichard, & Zuberbühler, 2006; Ouattara et al., 2009c; Zuberbühler, 2000), and recent studies highlighting the existence of combinatorial processes in contact calls confirm the importance of these abilities in animal communication

systems. Notably, forest-dwelling primates' flexible use of call combination involving identity-rich contact calls has been described. A study of Diana monkeys, a species closely related to Campbell's monkeys, revealed results analogous to those obtained here. Female Diana monkeys utter simple calls that can be combined with an arched structure that relates strongly to caller's identity (Coye et al., 2016). Females can produce either full or broken arches, their use depending on the immediate need for identity-cues (Candiotti, Zuberbühler, & Lemasson, 2012a). However, their communication system includes an additional layer of complexity as they can combine arched structures with three distinct call units instead of one only as Campbell's monkeys. These three units relate respectively to socio-positive, neutral and negative contexts and apparently function to refine the contextual information conveyed by combined calls (Candiotti et al., 2012a; Coye et al., 2016). Red-capped mangabeys (*Cercocebus torquatus*) present a similar example of context-related call suffixation. This species possesses two food call types, one threat call and one contact call type that varies with caller's identity. These four call types can be uttered alone or combined with an 'Uh' unit that is never uttered alone and which addition probably enhances vocal interactions (Bouchet et al., 2010).

Studies of phylogenetically more distant species also described communication systems based on context-related call combinations involving call units relating to caller's identity, suggesting that this capacity is likely to be widespread. Banded mongooses possess a combinatorial system that includes a close call that relates to caller's identity that can be emitted singly or combined with a second call unit. While the first 'identity' call unit does not change across contexts, the addition and acoustic structure of the second call unit relates consistently to caller's behaviour (digging, searching or moving; Jansen et al., 2012).

The presence of complex combinatorial call systems involving identity-related structures in these four highly social species supports the hypothesis that combination of vocal units is an

evolutionary answer to the need for complex social communication in spite of limited capacities of vocal production. All four species possess a flexible use of identity-related complex vocalisations depending on the behavioural and environmental context. However only the three primate species present a flexible use of calls combined in relation to the immediate social and vocal context (notably during vocal exchanges). Whether this is the consequence of enhanced social pressure and of primates' higher socio-cognitive abilities due to their strongly bond social groups remains to be explored.

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CHAPTER 6

SOCIOECOLOGICALLY-GUIDED DIVERGENCES BETWEEN TWO CLOSELY RELATED GUENON SPECIES' VOCAL BEHAVIOURS

Summary of article 4

Questions: Diana and Campbell's monkeys are two closely related and sympatric species of guenons living in the primary forests of West Africa. The populations of the Taï National Park (Cote d'Ivoire) have been subject to extensive long-term research tackling various aspects of their lives, from habitat use to social organization, through defence against predators and vocal communication. The vocal repertoires of female Diana and Campbell's monkeys are based on a set of homologous acoustic structures. The two species face similar ecological constrains but display distinct strategies to face those constraints, Campbell's monkeys being much more cryptic in many aspects of their lives. Non-human primates face strong limits over their vocal production, and vocal repertoires often reflects their phylogenetic position. But in the meantime, we may expect two related species with different social-ecological habits and thus potential different communicative needs to vary in the use they make of their shared calls. We conducted this study to investigate **whether the vocal communication of Diana and Campbell's monkeys reflect their distinct strategies in spite of their phylogenetic relatedness. And, if yes, to determine which aspects of their vocal behaviour differ?**

Methods: This article proposes a theoretical reflexion based on a review of the literature on Diana and Campbell's monkeys in the Taï National Park.

Results: The reviewed studies highlighted a set of socio-ecological features that likely co-evolved and gave rise to two close but yet distinct socio-ecological profiles. Indeed, Campbell's monkeys live in small, moderately dispersed groups and display less frequent and less diversified social interactions, with a smaller number of bonding partners. They have a smaller body size, are more exposed to ground dangers as they occupy low strata and adopt a clearly cryptic anti-predatory strategy when they are not in poly-specific troops. On the contrary, Diana monkeys live in groups twice bigger than Campbell's monkeys, spread over larger distances and behave very conspicuously regardless of the presence of heterospecific association partners. Females display more frequent and diversified interactions, involving more distinct bonding partners and Diana monkeys are considered 'dominant' (as opposed to the more 'subordinate' Campbell's monkeys) in the polyspecific 'supra-social' community they live in. In parallel, we highlight differences both in the structure of vocal repertoires and call use in these two species that are consistent with their distinct profiles. Firstly, both species possess derived alarm call types (*i.e.* absent from the other's

repertoire) but their overall acoustic structure differs. Campbell's monkeys possess several calls consisting of atonal structures with a narrow frequency bandwidth, whereas Diana monkeys use several frequency-modulated arched call types. Secondly, both species possess contact calls based on homologous acoustic structures, but Diana monkeys possess a richer set of combined calls, involving the combination of most vocal units of their repertoire. Thirdly, Diana and Campbell's monkeys show distinct patterns of call use. Indeed Diana monkeys are not only more vocal (*i.e.* call at higher rates) but they also use the most conspicuous combined calls (*i.e.* with a full arch) at higher rates and in higher proportion than Campbell's monkeys. On the contrary, the latter use cryptic structures (*i.e.* combined calls with a 'broken' arch and simple calls) more than Diana monkeys.

Conclusion: This article reviews subtle but likely important differences in the socio-ecology and vocal behaviour of Campbell's and Diana monkeys, two species that are often considered as relatively similar. The coherence between communication and socio-ecological characteristics is not surprising as we can reasonably think that all these factors have evolved and continue to evolve jointly, shaping each other in a complex dynamic loop. Importantly, this study shows that two species with roughly the same set of homologous acoustic structure can display very distinct vocal "strategies", depending on how they 'use' those structures. Here, Diana monkeys base a large part of their communication on conspicuous and identity-rich full arches, while Campbell's monkeys use more cryptic structure and combine call to a lesser extent. This suggests the possibility of relatively quick changes in communication systems as a result of combinatorial abilities since these do not require major neuro-anatomical changes in caller's phonatory system. Finally, although further testing will be required to determine the accuracy of the hypotheses proposed in this work, we believe that it further confirms the relevance of detailed analysis including call use to get a complete overview of animals' communication strategies.

Manuscript in preparation

Socioecologically-guided divergences between two closely related guenon species' vocal behaviours.

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ABSTRACT

As a result of strong genetic and neuro-anatomical constraints on non-human primates' vocal production, their vocal repertoires are generally considered as good indicators of phylogenetic proximity between primate species. However, closely related species do not necessarily have the same communication needs as a result of different socio-ecological and this may impact the use they make of their vocal structures. This study focussed on Diana and Campbell's monkeys, two sympatric and closely related species of guenons. They possess the same basic repertoire of acoustic structures and face similar ecological constrains but display clearly distinct strategies to face those constraints, Campbell's monkeys being much more cryptic than Diana monkeys in various aspects of their behaviour. We reviewed the socio-ecological characteristics and female vocal communication of both species collected from long-term surveys to determine whether and how their vocal behaviour reflect these different strategies. The analysis revealed differences between species at several levels of their communication that were consistent with their socio-ecological profiles. Importantly, the shared acoustic structures were used differently by each species according to their degree of crypticity *vs* potential to encode individual identity. Striking differences lied in the distinct acoustic structures used as alarm calls, in the contact call subtypes preferentially used and in the richness of the call combination patterns. This study confirms that closely related species with similar environmental and articulatory constraints can develop distinct vocal systems via flexible call use and combinatorial patterns. Hence, more comparative studies should include these frequently overlooked yet relevant aspects of animals' vocal communication and go beyond the description of acoustic repertoires.

Key words: wild guenons, call combination, identity-related vocalisations, call use

Chapter 6: Comparison of female Campbell's and Diana monkeys' vocal behaviour

INTRODUCTION

Communication in the animal kingdom is ubiquitous, and often plays a central role in major functions such as reproduction (Catchpole, 1987; Delgado, 2006), territory defence (de Kort, Eldermire, Cramer, & Vehrencamp, 2009), signalling danger to conspecifics (Macedonia & Evans, 1993; Zuberbühler, 2009) as well as regulation of social relationships and spatial distribution of individuals within (Radford & Ridley, 2008; Waser, 1975) and between groups (Da Cunha & Byrne, 2006). Its essential role for the survival and daily life of many species suggests that it evolved under strong selective forces. Three factors seem to have influenced the evolution and the diversification of communication signals: habitat, predation and social life (Catchpole, Slater, & Song, 1995; Freeberg, Dunbar, & Ord, 2012). First, the animals' habitat can influence the sensory modality of communication as visually dense habitats (*e.g.* turbid water, dense forests) favour acoustic communication (P. Marler, 1967). In addition, signal deterioration due to propagation constraints and ambient noise can shape the acoustic structure (frequency, amplitude or intensity, as well as degree of gradation) of vocal signals (Brown & Waser, 1988; Marler, 1967; Marten & Marler, 1977; Waser & Brown, 1986). Second, predation risk can influence the diversity of signals used, as signalling the imminence of danger or the type of predator could be beneficial (Blumstein, 1999a, 1999b; Furrer & Manser, 2009; Macedonia & Evans, 1993); it could also influence the structure of acoustic signals, as some signals might have evolved so as to be less easily detected by predators (*i.e.* acoustic crypsis) (Morisaka & Connor, 2007; Ruxton, 2009) and their use as some species remain silent to 'hide' from hunting predators (Scott McGraw, Zuberbühler, & Noë, 2007; Ruxton, 2009). Finally, social complexity is considered as an important driver of communication complexity (Freeberg et al., 2012; Houdelier, Hausberger, & Craig, 2012; McComb & Semple, 2005). Indexes of social complexity correlate positively with size of vocal repertoires, information content -particularly the potential of a call to signal caller's identity-,

and calling rates (Bouchet, Blois-Heulin, & Lemasson, 2013; Kroodsma, 1977; Manser et al., 2014; McComb & Semple, 2005).

Hence, animals' vocal behaviour seem to be the result in a balance between social needs (*e.g.* maintaining socio-spatial cohesion, signalling danger or attracting mates), and propagation and eavesdropping constraints linked to habitat and predation. In addition, the diversity of a given species' acoustic structures depends on its phylogenetic position, as its genetic and neuro-anatomical characteristics determine both the organisation and flexibility of its vocal repertoire (Chen & Jürgens, 1995; Gautier, 1988; Hahn, Hewitt, Schanz, Weinreb, & Henry, 1997; May-Collado, Agnarsson, & Wartzok, 2007; Ord & Martins, 2006; Wilczynski & Ryan, 1999).

Here, we investigated the vocal behaviour of adult females of two species which apparently face similar constraints: Diana (*Cercopithecus diana*) and Campbell's (*Cercopithecus campbelli*) monkeys (see Table 1 for details and references). These two sympatric, territorial and arboreal guenon species live in dense tropical forests in West Africa. We review long-term studies of their Taï National park populations that share the same habitat and face the same predators, *i.e.* leopards (*Panthera pardus*), crowned hawk eagles (*Stephanoaetus coronatus*), chimpanzees (*Pan paniscus*) and humans. In this area, Diana and Campbell's monkeys regularly form polyspecific troops with six other primate species: lesser spot-nosed monkeys (*Cercopithecus petaurista*), olive colobus (*Procolobus verus)*, red colobus (*P. badius*), black and white colobus (*Colobus polykomos*), sooty mangabeys (*Cercocebus atys*) and, to a lesser extent, putty-nosed monkeys (*C. nictitans*). The function of these polyspecific communities seems to be primarily to increase protection against predators (Mcgraw & Zuberbühler, 2008; Noë & Bshary, 1997). Campbell's and Diana monkeys live in harem groups in which the adult male remains peripheral and defends the group against intruders while females form the social core of the group. Adult males and females possess distinct vocal repertoires (Table 1). These two species diverged 3.5 million years ago and the Diana monkey is the most closely related

species to the Mona superfamily to which Campbell's monkeys belong. As a probable result of their phylogenetic proximity (Geissmann, 2002; Meyer et al., 2012), vocal repertoires of the females of these two species are based on a set of homologous acoustic structures: atonal units emitted in short repetitions, low pitched quavers, high-pitched trills and arched frequency modulations (Candiotti, Zuberbühler, & Lemasson, 2012a; Gautier, 1988; Lemasson & Hausberger, 2011).

However, although these two species face similar constraints, they have adopted different strategies to cope with them (see Table 1 for a synthesis of their socio-ecological differences and references). Campbell's monkeys are cryptic and uneasy to detect even at a relatively close range because of their olive-grey coats and cryptic locomotion. Their groups are relatively small (9.3 individuals on average) and group members are rarely more than 25 meters apart. Inter-group and intra-group social interactions are rare. Campbell's monkeys use mostly the lower forest strata (*i.e.* from the ground to to 5 meters high where they spend 30% to 50% of their time depending on the authors (Buzzard, 2006b; McGraw, 2007). Females typically stop moving and hide when a ground predator attacks (Ouattara, Lemasson, & Zuberbühler, 2009a). As they are the smallest diurnal primates in Taï, Campbell's monkeys seem to occupy a 'subordinate' position in the Taï polyspecific communities (*i.e.* their food is stolen or they are chased by other primates) and they probably experience strong competition from other primate species. On the contrary, Diana monkeys are very conspicuous, twice as large as Campbell's monkeys, they have brightly coloured hair and their locomotion (*i.e.* running and leaping) is boisterous. Their groups average 23.5 individuals which often spread over 25 to 50 meters but they interact frequently, and spend most of their time in the medium and higher forest strata (*i.e.* 5-20 m and > 20m from the ground). Diana monkeys occupy a central place in the Taï community; several species actively maintain association with them, following them when on

the move. They are called the forest 'sentinels' because they detect danger faster and from greater distances than the other species.

Our study compares female Campbell's and Diana' communication systems to evaluate to what extent their socio-ecological strategies are reflected in their vocal behaviour. We were particularly interested in what use these two species make of the different acoustic structures they are sharing in their repertoire. To provide a complete picture, we reviewed and discussed both the similarities and the differences that can be highlighted between female Diana and Campbell's monkeys' vocal behaviours.

Table 1: Summary of the main socio-ecological characteristics of Campbell's and Diana monkeys. Grey background highlights traits for which the two species display similar characteristics, white background highlights traits for which Campbell's and Diana monkeys differ.

	Characteristic	Campbell's monkeys	Diana monkeys	Reference
Morphology	Sexual dimorphism: Body size	Yes		McGraw et al., 2007, pp. 21–24
	Sex difference: Vocal repertoire	Yes		Gautier, 1988; Gautier & Gautier, 1977; Ouattara et al., 2009a; Zuberbühler, 2002
	Body weight	♂: 4.5 kg; ♀: 2.7 kg	♂: 5.2 kg; ♀: 3.9 kg	Oates et al., 1990
	Body aspect	Grey and white, dully and poorly contrasted colours	Black, white and red, bright and highly contrasted colours	Kingdon, 2015; McGraw et al., 2007, pp. 21–24
Ecology	Habitat	Dense tropical forest		Gatinot, 1974; Lernould, 1988
	Predators	Leopard, crowned-hawk eagle, chimpanzee and human		Mcgraw & Zuberbühler, 2008
	Diet	Fruit: 46% Prey: 33% Foliage: 8%	Fruit: 59% Prey: 16% Foliage: 16%	Buzzard, 2006b
Spatial distribution	Locomotor profile	Quadrupedal		McGraw, 1998; McGraw et al., 2007, pp. 223–250
	Cryptic locomotion during travel	Yes	No	McGraw et al., 2007, p. 21; 248
	Preferred strata	Ground and low (< 5m)	Medium and high (> 5m)	Buzzard, 2006b, p. 200; McGraw, 2007
	Average group spread	<25 m	< 50m	Wolters & Zuberbühler, 2003
Heterospecific interactions	Percentage of time forming polyspecific groups	76%	86%	Galat & Galat-Luong, 1985
	Supra-social position in the polyspecific association	"Subordinate"	"Dominant"	Buzzard, 2006a; Scott McGraw et al., 2007, p. 22

Intra-specific: Intergroup interactions	Group density	2.5 groups/km²	2.6 groups/km²	Buzzard & Eckardt, 2007; Galat & Galat-Luong, 1985; Ouattara, Lemasson, & Zuberbühler, 2009b
	Home range size	56 ha	56.8 ha	
	Population density	24 ind. /km²	62 ind. /km²	Buzzard & Eckardt, 2007
	Frequency of intergroup encounters (N per day)	0.033	0.358	
	Aggressive inter-group encounters (%)	67%	35%	
Intra-specific: Intragroup interactions	Social structure	Harem		Buzzard & Eckardt, 2007; Candiotti et al., 2015; Ouattara, Zuberbühler, N'goran, Gombert, & Lemasson, 2009; Candiotti et al, 2015
	Female philopatry	Yes		
	Male's position in the group	Socially isolated		Buzzard & Eckardt, 2007; Alban Lemasson, Blois-Heulin, Jubin, & Hausberger, 2006; Rowell, 1988
	Generation overlap	3 to 4 generations of offspring		Buzzard & Eckardt, 2007
	Group size (number of adult females)	9.3 (5.3)	23.5 (11.5)	Buzzard & Eckardt, 2007; Ouattara et al., 2009c
	Spatial proximity (% of observation time)	0.8 %	1.25 %	Candiotti et al., 2015
	Grooming (% of observation time)	0.65 %	1.9 %	Candiotti et al., 2015
	Rate of agonistic interactions (/h)	0.001	0.0055	Candiotti et al., 2015
	Coalition between females	+	++	Buzzard, 2004; Lemasson et al, 2006; McGraw et al, 2007, p. 59
	Differentiated bonds between females	+	++	Candiotti et al., 2015

1. Diana and Campbell's monkeys' vocal communication

We took into account as many relevant characteristics as possible; thus, we included both vocal production (*i.e.* acoustic structure, number of distinct vocal units, calls' potential to convey information about caller's identity), and vocal use (*i.e.* call combination, call rate and function; Table 2).

a. Similarities and variability of Diana and Campbell's monkeys' acoustic structures

i. Homologous acoustic structures of the two vocal repertoires

Figure 1 shows sonograms of the calls given by free-ranging female Diana and Campbell's monkeys in the Taï forest. The vocal repertoires of Diana and Campbell's monkeys clearly rely on similar sets of homologous acoustic structures (Fig. 1). Both species emit calls consisting of the rapid repetition of a short unit, involving chevron-shaped (RRC/Brr) and atonal (RRA/R) structures. These structures function respectively as threat (RRC/Brr), alert (RRA) or 'discomfort' calls (R). Similarly, they possess homologous contact call structures: both species emit high-pitched trills (*i.e.* ST/H calls) as well as low-pitched quavers (SH/L calls). In addition, these structures can be emitted alone or combined with arched units to form CH and LA combined calls. Both species possess two combined call subtypes which include either a full arch (*i.e.* CHf and LAf calls) or a broken (incomplete) arch (*i.e.* CHb and LAb calls) (Candiotti et al., 2012a; Lemasson & Hausberger, 2011). The fact that both species have the same number of distinct acoustic units in their repertoires (Table 2) confirms that Diana and Campbell's monkeys possess equivalent acoustic production capacities.

ii. Homologous potentials for coding individual identity

A broad range of taxa possess identity-rich calls (*e.g.* birds: Aubin & Jouventin, 2002; nonhuman primates: Rendall, Rodman, & Emond, 1996; terrestrial mammals: Müller & Manser, 2008; see Kondo & Watanabe, 2009 for a global review), and the ability to signal one's identity through its

vocal utterances can be essential for animal communication, notably in social contexts. Females form the social core of guenon groups, and this ability likely plays an important role to maintain the socio-spatial cohesion of groups in their visually dense habitat (Byrne, Conning, & Young, 1983; Candiotti et al., 2015; Cords, 2002; Lemasson, Hausberger, & Zuberbühler, 2005; Rowell, 1988). The potential to code caller's identity can vary with the function of calls. Indeed calls given in undisturbed contexts (*e.g.* socio-positive interactions) are less stereotyped and more variable between callers than urgent signals (*e.g.* alarm calls) (Bouchet et al. 2013). In addition, the identity coding potential (PIC) of female Campbell's monkeys calls presents a gradation between call types: calls' PIC was the lowest in repetitive atonal structures (*i.e.* RRC and RRA) and increased from trills (ST calls) and quavered structures (SH calls) to combined calls (CH), the latter having the highest PIC. The fact that this gradation of call PIC is consistent with reports investigating the emission context of contact calls by Campbell's monkeys indicates that females' use of distinct contact call types (*i.e.* simple or combined) depends on the immediate context and the need to associate an indication of their identity (Coye, Arlet, Ouattara, Lemasson, & Zuberbühler, In prep.).

Diana monkeys possess a similar set of calls but detailed acoustical analyses are lacking for this species. Hence, we can only hypothesize that due to the strong structural homologies between the two species' contact calls, a similar gradation exists. This hypothesis is supported by the fact that, as for Campbell's monkeys, the comparison of acoustic structures of LA combined calls within- and between-callers suggests that these calls possess a high potential to signal identity (Candiotti, Zuberbühler, & Lemasson, 2012b).

As no studies compared the relative potential to signal identity of combined calls between these two species, we made a complementary evaluation using an automated classification of CHf and LAf calls using Artificial Neural Networks (ANNs) (see chapter 2 section 6 for details). Our preliminary results show that combined arched calls can be associated with a high confidence level to a given caller. The procedure, similar to that adopted by Mielke & Zuberbühler (2013) consisted in training several ANNs on a set of calls from identified emitters before testing the accuracy of classification with

"new" calls (*i.e.* given by the same individuals but not used during the training phase). A preliminary analysis involved three adult females of each species, for which we included 19 to 28 calls per individual (mean ± SE: 23 ± 1.57 calls) and averaged the classification of 15 artificial neural networks for a sample of 24 calls (*i.e.* 4 per individuals) that were not part of the training set. The results obtained with this method showed similar performances for classification of CHf and LAf calls, with 91.7% accurate classification for both call types. Equivalent proportions of accurately classified calls of the two species, obtained with the same procedure suggest that these homologous call types have equivalent potentials to convey caller's identity.

Finally, the relevance to receivers of between-caller variations of call structure was confirmed by playback experiments that demonstrated that adult females of both species are able to recognize members of their group based on the structure of these vocalisations (Coye, Zuberbühler, & Lemasson, 2016; Lemasson et al., 2005).

Table 2: Summary of the main traits characterising the vocal behaviour of wild Diana and Campbell's monkeys. Parameters for which species differ importantly are marked in bold.

Vocal feature	Characteristic	Campbell's monkey	Diana monkey	Comparison	Reference
Call structure	Number of distinct acoustic units	8	8	Campbell = Diana	Candiotti et al., 2012a; Coye, Ouattara, Zuberbühler, & Lemasson, 2015; Lemasson & Hausberger, 2011; Ouattara et al., 2009c; Zuberbühler, Noë, & Seyfarth, 1997
	Potential for acoustic identity coding	YES (arched unit)	YES (arched unit)	Campbell = Diana	Bouchet et al., 2013; Candiotti et al., 2012b; Lemasson & Hausberger, 2011; Lemasson, Ouattara, Petit, & Zuberbühler, 2011
	Individual auditory recognition	YES	YES	Campbell = Diana	Coye et al., 2016; Lemasson et al., 2005
	Number of derived vocalisations	4	**7**	Campbell < **Diana**	Candiotti et al., 2012a; Coye et al., 2015; Lemasson & Hausberger, 2011; Ouattara et al., 2009c; Zuberbühler et al., 1997
	Total number of call types	8	**16**	Campbell < **Diana**	
Call use	Number of combined call types	2	**8**	Campbell < **Diana**	Candiotti et al., 2012a; Coye et al., 2015; Lemasson & Hausberger, 2011; Ouattara et al., 2009c; Zuberbühler et al., 1997
	Number of units which can be combined with others	3	**7**	Campbell < **Diana**	
	Individual call rate (calls per hour, per individual)	**SH: 0.85** ST: < 0.73* - CH: 7.56	L: 0.51 **H: 1.27** **A: 17** **LA: 19.9**	**Campbell's** > Diana Campbell's < **Diana** Campbell's < **Diana** Campbell's < **Diana**	Coye et al., In prep ; Candiotti et al., 2012a
	Predominant arched sub-type	**Broken**	**Full**	**Campbell's ≠ Diana**	

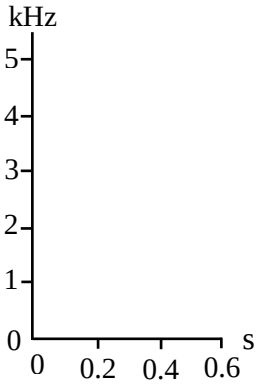
b. Comparisons between Diana and Campbell's monkeys' vocal behaviours

i. Vocal production: "Derived" vocalisations

Significant acoustical and functional differences exist between the two species (Figures 1 and 2). Each species possesses "derived" vocalisations (*i.e.* absent from the other's repertoire (Gustison, Roux, & Bergman, 2012). However these vocalisations do not concern the same acoustic structures (Fig. 2). On the one hand, Campbell's monkeys possess several low-pitched repetitive atonal calls that differ either in the number of units uttered or in the frequency of the units (Ouattara et al., 2009c): RRA1, RRA3 and RRA4 calls, emitted respectively to signal general danger, eagles and leopards, whereas Diana monkeys possess only one repetitive atonal call (*i.e.* R) emitted in 'uncomfortable' situations (*e.g.* stressful social situations and low-threat disturbances). On the other hand, Diana monkeys possess three types of arched calls (A, Alk, W) emitted in social (A call) and alarm contexts (Alk and W calls) respectively (Candiotti et al., 2012a; Coye et al., 2015; Zuberbühler et al., 1997). Alk and W calls resemble an "A" call with the lower frequencies truncated. More precisely, "Alk" calls are only composed of this truncated arched structure (Zuberbühler et al., 1997) whereas "W" calls are composed of a short, high-pitched and arched-shaped note preceding the truncated arched structure (Fig. 1, C. Coye and A. Candiotti unpublished data). Campbell's monkeys use arched structures, but they possess only one type (*i.e.* homologous to A units), always used in combination with a SH call (*i.e.* CH calls).

Hence, although both species seem to have evolved derived alarm calls (*i.e.* RRA subtypes *vs* Alk and W subtypes) through diversification of pre-existing structures in their repertoire, the acoustic structures from which they derived differ (*i.e.* low-pitched repeated units *vs* frequency-modulated arches). Campbell's monkeys emit more "cryptic" acoustic structures more frequently, while Diana monkeys use preferentially calls with a large frequency bandwidth and higher intensity.

(a)



Species	Simple calls					
	Repetitive chevron-shaped calls	Repetitive atonal calls	Low-pitched quavered calls	High-pitched quavered calls	Blunt arch calls	Sharp arch calls
Diana monkey	Brr	R	L	H	Af, Ab	Alk, W
Campbell's monkey	RRC	RRA1, RRA3, RRA4	SH	ST	-	-

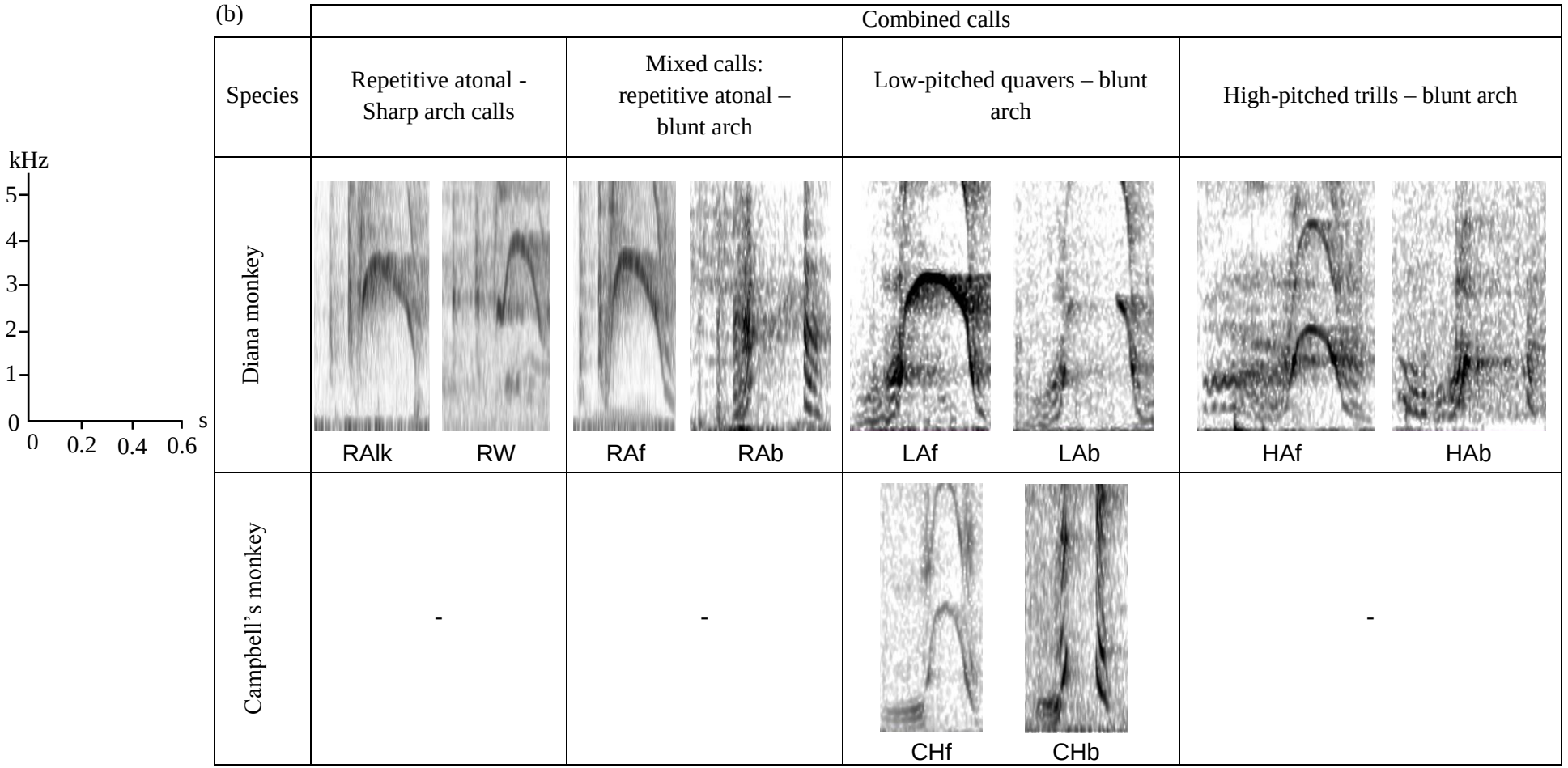


Figure 1: Acoustic structural homologies in the vocal repertoires of Diana and Campbell's monkeys, illustrated by spectrographic presentations of all simple (a) and complex calls (b) uttered by adult females. We used the names as originally published (Candiotti et al., 2012a; Lemasson et al., 2005; Ouattara et al., 2009) to facilitate cross-reading. This representation omits call types used only in very rare occasions, *i.e.* alarm calls given by females in extremely urgent situations and which resemble roughly to the male alarm calls in each species (*i.e.* described elsewhere as Wak-oo and Hok' in Campbell's monkeys (Ouattara et al., 2009), and 'leopard' and 'eagle' alarm calls in Diana monkeys (Zuberbühler et al., 1997).

ii. Call use

Combinatorial abilities

Diana monkeys' vocal repertoire is larger than that of Campbell's monkeys (Figures 1 and 2, Table 2), in spite of their equivalent acoustic production capacities. This difference is undoubtedly the consequence of Diana monkeys' greater combinatorial abilities as they use almost every call type in their repertoire either alone or in combination with other structures, whereas Campbell's monkeys possess only two combined call sub-types (*i.e.* CHf and CHb) (Fig. 1). Diana monkeys combine call units non-randomly and systematically merge a "non-arched" introductory unit (*i.e.* H, L or R) with an arched structure (*i.e.* Af, Ab, Alk or W). Diana monkeys also possess 'mixed' call types (*i.e.* combinations of functionally different calls) mixing call units emitted in distinct contexts (*i.e.* socio-positive, socio-negative and alarm, Fig. 2).

Combined calls are uttered consistently in contexts which correspond to the cumulated contexts of emission of the units alone (*i.e.* as single calls): while the introductory unit relates to the valence of the context for the caller, the second unit signals caller's identity. H, L, and R units (uttered respectively in socio-positive, neutral and negative contexts) can all be combined with A calls (uttered in a broad range of contexts but encoding individual identity) into HA, LA and RA combined calls, uttered in socio-positive, neutral and negative contexts respectively (Candiotti et al., 2012a). In line with this, Alk and W calls (which are uttered only in urgent, predatory contexts) are combined only with R units (negative contexts) (Coye et al., 2015).

A recent experimental study using artificial LA and RA stimuli produced by re-combination of call units initially uttered separately demonstrated that combined calls consist of the linear combination of two call units and are meaningful for the receiver. The replacement of one unit by another (*e.g.* replacing L by R or replacing the A call of a group member by the A call of a female from a neighbouring group) consistently modified the receiver's reaction that was according to prediction (Coye et al., 2016).

These data suggest that Diana monkeys possess a compositional system, involving call combinations in various contexts and allowing important diversification of possible messages. Combined calls systematically involve arched structures and their over-representation in Diana monkeys' communication system compared to Campbell's monkeys' communication system is consistent with the opposite patterns for derived alarm calls detailed above.

Call rates and preferred call types

As previously mentioned, Diana monkeys behave conspicuously while Campbell's monkeys seem to adopt a more cryptic strategy (Table 1). This opposition is also true for their vocal activities as the call rates and the proportions of various calls (*i.e.* average number of calls uttered per hour) differ between these two species.

Diana monkeys are significantly more vocal than Campbell's monkeys (emitting 3 times more alarm calls and 4.5 times more contact calls; Table 2). The only call type that Campbell's monkeys emit at higher rates than Diana monkeys is the cryptic SH/L call (Fig. 1, Table 2) as it represents respectively 10% and 1% of the contact calls given by females of each species. Comparisons of preferred arched subtypes reveal that Campbell's monkeys use preferentially the broken subtype (which represents 79% of the total arched structures emitted), whereas Diana monkeys use preferentially full arches (which represent 72% of LA calls, homologous to Campbell's CH call). A previous study hypothesized that complete arched structures, because of their higher top frequency (and often higher intensity of emission), could be detected more easily than broken arched structures because they fall in the most sensitive hearing range of monkeys' predators (Coye et al., In prep.). This different use of combined calls by female Diana and Campbell' monkeys further reinforces the dichotomy between their communication systems.

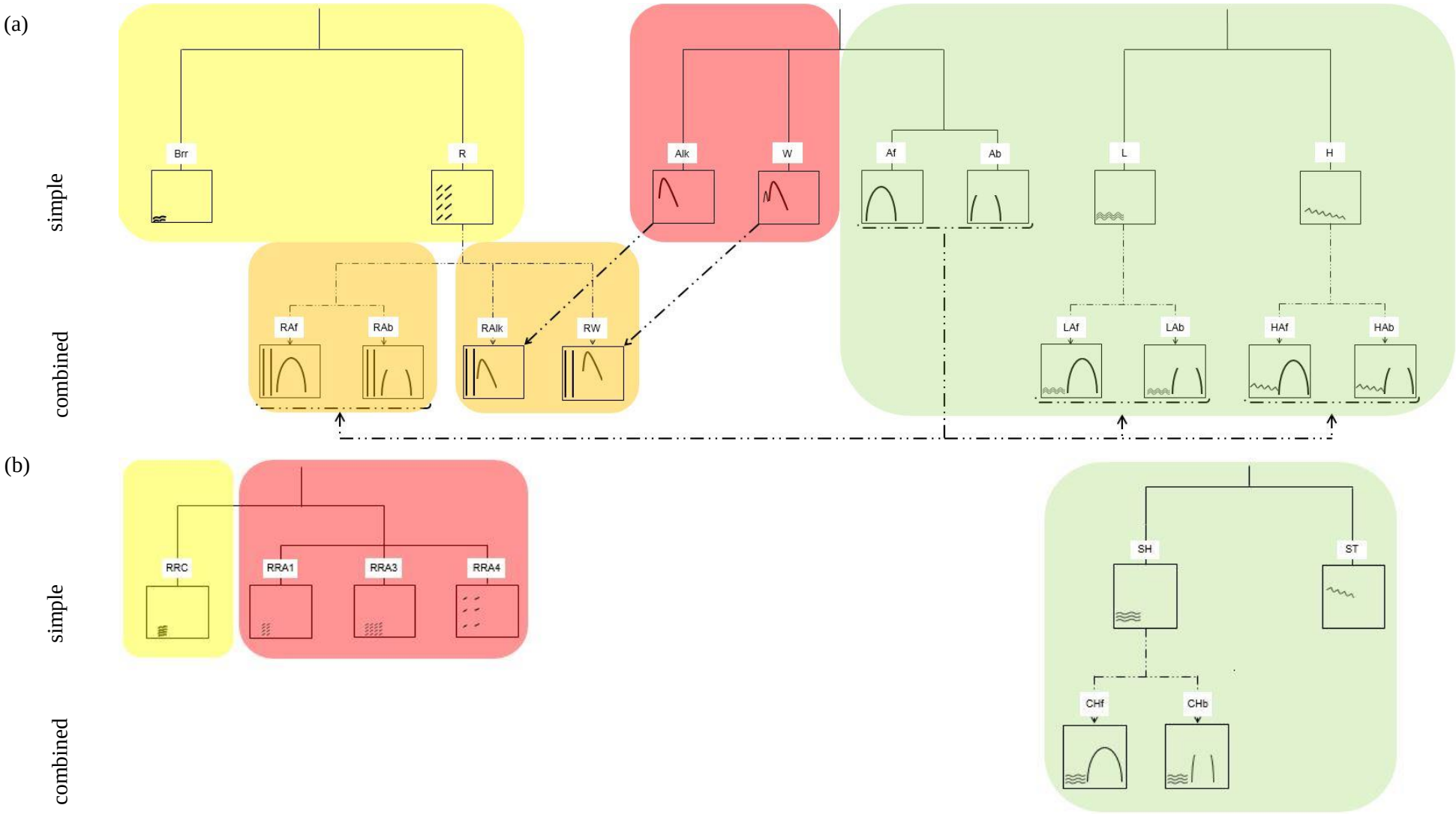


Figure 2: Schematic trees representing the vocal repertoires of Diana (a) and Campbell's (b) monkeys. On both plots, the line entitled "simple" shows calls consisting of a single unit, the line entitled "combined" shows calls composed of several calls combined together. Simple calls were plotted into the same tree when presenting close acoustic structures. Combined calls involves the simple calls as indicated by arrows. Shadings show the general function of calls, with green shading for socio-positive contact calls, yellow shading for socio-negative calls and red shading for alarm calls. Orange shadings show combination of calls from different functional categories (mixed calls).

DISCUSSION

Campbell's and Diana monkeys adopt very distinct socio-ecological strategies to cope with similar environmental constraints. The vocal repertoires of these two species are based largely on shared homologous acoustic structures as a result of their phylogenetic proximity. However, their distinct strategies are associated with communication systems that exploit this basic set of acoustic structures fairly differently. The fact that Campbell's monkeys are small-bodied, live in small and compact groups close to the ground, are often chased by other primates in their community and are thus more exposed to danger, might explain their cryptic behavioural profile. In line with this, their derived alarm calls are based on inconspicuous low-pitched structures (*i.e.* RRA). Their use of contact calls also reflects this acoustically cryptic strategy as their use of call combination involving arched structures is limited, and they are less vocally conspicuous because they call at lower rates and because they use preferentially less detectable structures (*i.e.* simple SH calls and broken CHb combined calls). On the contrary, Diana monkeys live in larger groups that spread over relatively large distances in higher forest strata, and their anti-predator strategy does not seems to rely on predator avoidance through cryptic behaviour but more on early predator detection. Their derived alarm calls are based on conspicuous and loud arched structures which propagate over long distances. Here again, females' call use is consistent with their global profile: Diana monkeys use various combined call types emitted in distinct contexts that systematically involve an arched structure. Finally, females of this species emit contact calls at higher rates and use full arches (that strongly relate to caller's identity) more than do Campbell's monkeys. The analysis of emission context of call types can throw light on their function and sometimes allow us to hypothesize about the selective pressures that influenced their emergence. Previous studies show that the type of call emitted by female Campbell's and Diana monkeys varies partly with the need to signal caller's identity as both species used full arches more in such situations (*e.g.* when the number of

individuals around was high or when visibility was poor). However, Campbell's monkeys' need to signal identity seems balanced in a trade-off with the need to remain cryptic and avoid predation notably through the use of acoustic crypsis (*i.e.* calls limiting probability of being detected by predators). On the contrary, Diana monkeys' rates of conspicuous arched contact calls increased with predation threat, suggesting that Diana monkeys' contact calls function to avoid predation in a system of co-ordinated vigilance.

Non-human primates' vocal repertoires are determined by genetic and neuroanatomical constraints which evolve relatively slowly, as demonstrated by studies reconstructing the phylogeny of primate taxa on the basis of species' vocalisations (Gautier, 1988; Geissmann, 2002; Meyer et al., 2012). Variations of the use of closely related species' homologous acoustic structures are susceptible to take place more rapidly than distinct call structures. Although several reports address animal vocal communication from a comparative point of view, different uses of homologous structures and their rates of emission are rarely taken into account (*e.g.* Blumstein, 2003; Pollard & Blumstein, 2012). Our review suggests that future studies should take these overlooked aspects of a species' vocal behaviour into account as they are susceptible to play very important roles in animals' daily life and should provide further insights concerning communication strategies and socio-ecological profiles.

Two studies conducted on *Herpetidae* and non-human primates respectively investigated the possible influence of social complexity on communication complexity included the presence and diversity of combined structures as well as call use into account. Interestingly, in addition to highlight 'classical' variation in the number of call types in the repertoire (*e.g.* Blumstein, 2003; Blumstein, 1999b; Kroodsma, 1977), and in the presence of identity-rich structures with the complexity of species social life or group size (*e.g.* birds: Wilkinson, 2003; Houdelier et al., 2012; Jouventin & Aubin, 2002; Mathevon, Charrier, & Jouventin, 2003; sciurids: Pollard & Blumstein, 2012), these studies revealed differences in call use, and call combination. In

particular, Manser and collaborators showed that if calls given in repetitive sequences were present in all the species studied, the three social obligate species with more complex social lives than solitary or facultative social mongoose species (*i.e.* banded mongooses, dwarf mongoose and meerkats) further combine distinct call types into larger utterances and sequences that appear to convey a different meaning (Collier, Radford, Bickel, Manser, & Townsend, 2016; Manser et al., 2014). The study conducted on non-human primates compared three cercopithecids species (*i.e.* De Brazza Monkeys (*C. neglectus*), Campbell's monkeys and red-capped mangabeys) living respectively in small family group of 3 to7 individuals, harem group of 7 – 13 individuals and in multi-male multi-female groups of 19 to 21 individuals. It showed that the global rate of calling, as well as the number of distinct combined patterns produced as well as the frequency at which combined calls were used reflected the differences in social complexity between these species.

Freeberg and collaborators (2012) proposed to define complex social systems as "those in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time". According to this definition Diana monkeys' social life is more complex than that of Campbell's monkeys (Table 2). Rates of Diana monkeys' affiliative (*i.e.* grooming and sitting near each other) and agonistic interactions between females are twice those of Campbell's monkeys. Furthermore, female Diana monkeys' social relationships are more differentiated (*i.e.* involving coalitions and strongly preferred affiliative partners) than those of female Campbell's monkeys. Finally, Diana monkeys' interactions with neighbouring groups of conspecifics are more frequent and more variable than those of Campbell's monkeys (Table 2). Hence, the co-occurrence of increased social complexity and increased combinatorial abilities in Diana monkeys supports the hypothesis that combinatorial abilities evolved with increasing social needs, and allowed a more diverse communication system and increased

repertoire size (Manser et al., 2014). Our results underline clearly the intricate impacts of various factors in a dynamic loop and further studies investigating the relationship between the presence and use of combinatorial structures in the repertoire of other cercopithecids will be required to conclude more firmly about the relative influence of the distinct pressures evoked.

Globally, this study highlights that two closely related species with distinct strategies to cope with similar environmental and articulatory constrains can develop distinct vocal systems via flexible call use and combinatorial patterns. Interestingly, here, call combination gave rise not only to a diversification of socio-positive calls, but also to extended alarm and "mixed" calls systems which allow animals to convey more subtle and complex messages. We believe that the question of meaning relating to combined structures and their components is central. To go further, researchers need to extend this type of analysis to species with various levels of vocal plasticity and to species which might have taken distinct evolutionary paths to cope with socially complex living conditions. Indeed, some bird species produce meaningful call combinations that reveal combinatorial abilities identified as compositional syntax (Suzuki, Wheatcroft, & Griesser, 2016) or phonemic contrast (Engesser, Crane, Savage, Russell, & Townsend, 2015), but other species, although they emit complex call sequences, seem to lack organisational rules (Kroodsma, 1977; Riesch, Ford, & Thomsen, 2008) leading to consistent modification of calls' meaning and further research will be required to determine which factors influenced the evolution of these distinct systems.

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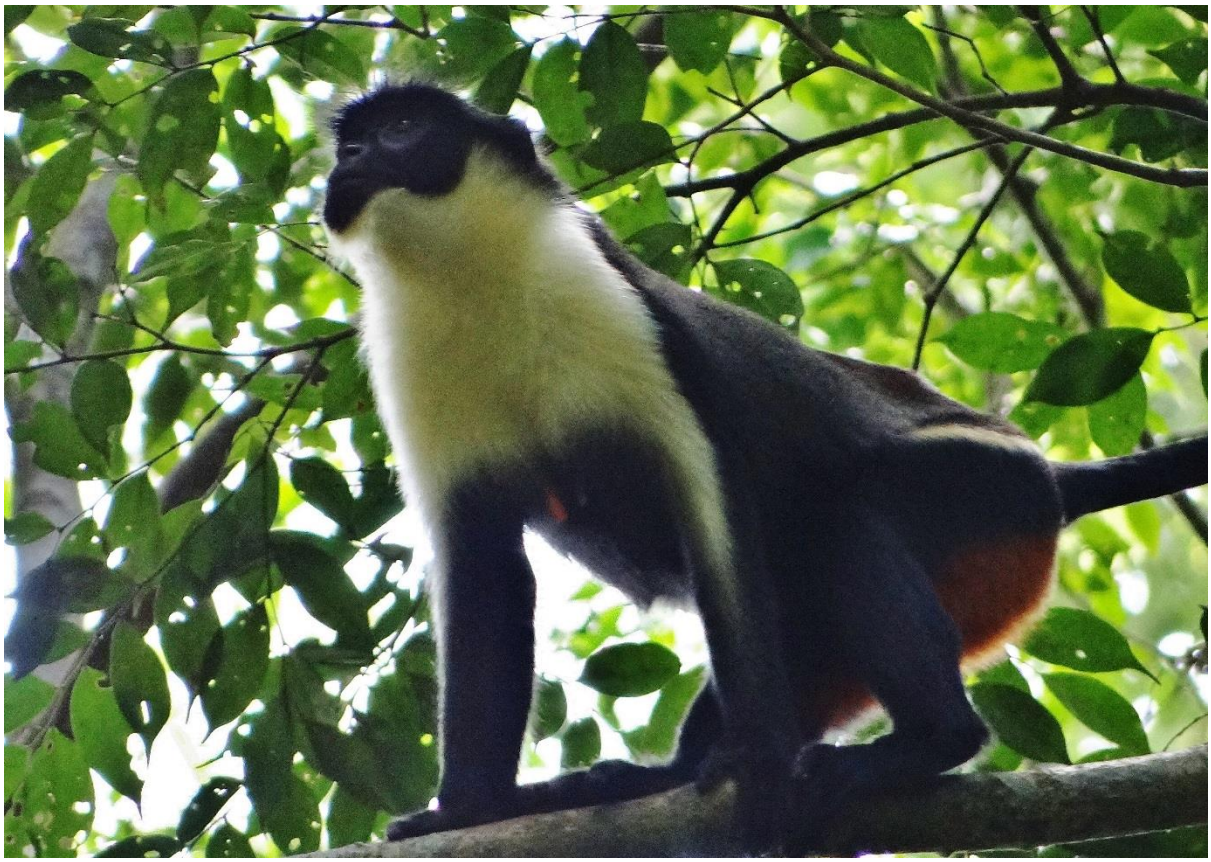
CHAPTER 7

GENERAL DISCUSSION



7. General discussion

7.1. Summary of the main findings

This thesis comports two complementary parts, investigating the topic of call combination with distinct approaches. The first part, based on experimental studies, aimed at verifying the relevance to receivers of combinatorial mechanisms in the calls of Campbell's and Diana monkeys (chapters 3 and 4). The second part focused on socio-ecological factors influencing call emission and combination, based on intra- (chapter 5) and inter- (chapter 6) specific comparative approaches.

The first two studies involved a playback experimental approach and shared close rationales. Indeed, in both cases, we used artificially recombined stimuli to test the relevance to receivers of variations in the information content resulting from combination of vocal units. These studies confirmed the existence of call combination in both male Campbell's monkeys and female Diana monkeys. More importantly, they demonstrated robustly the functional relevance of call combination, as changes in call composition consistently induced changes in receivers' reaction according to the predictions from observational studies that showed a relationship between context and use of simple or combined calls. Those results are also biologically relevant because they were systematically based on the spontaneous reaction of wild (untrained) individuals to calls naturally occurring in their daily life. In the examples described here, call combination allows animals to increase the diversity of messages conveyed by their calls using only a small number of distinct vocal units in both alarm and social contexts. In guenons, males and females possess distinct vocal repertoires and play very different roles in the group, the former being the "vigilant" sex and the latter being the "social" sex (Byrne, Conning, & Young, 1983; Candiotti et al., 2015; Cords, 2002; Rowell, 1988). Our experiments confirmed the relevance of call combination in males' alarm calls and females' contact calls that are the respective cores of their communication. Indeed, in males, our experiment showed

that Krak and Krak-oo alarm calls of Campbell's monkeys are based on the same 'Krak' stem to which the addition of an 'oo' suffix attenuates the related emergency. In females, we showed that the L, R and A calls of Diana monkeys are combined into calls that convey linearly the information of the units composing them (*i.e.* emotional valence of the context, callers' identity).

These results are in line with the hypothesis exposed in the introduction of this work, which suggests that, because non-human primates possess limited articulatory capacities, flexible combination of vocal units might have been selected to fulfil animals' communicative needs. In particular, we brought experimental evidence for the existence of morphology-like functional combination in both species.

The second part of this thesis focused on the vocal communication of females in Diana and Campbell's monkeys. It involved two studies based on distinct approaches to investigate the vocal correlates of socio-ecological factors respectively on a short-term and on an evolutionary timescale: the first study was based on observational data and aimed to clarify the contexts of emission of contact calls in female Campbell's monkeys. The second study was a theoretical review analysing comparatively the vocal communication of female Diana and Campbell's monkeys. In both studies, the first goal was to analyse the flexible use of calls in free-ranging adult females with special attention paid to combinatorial features. Secondly, these studies proposed to shed light on some possible functions of combined calls and to formulate hypotheses about the selective forces driving their evolution thanks to detailed analyses of calls' context of emission and use by contemporary species' representatives. Our results highlighted that flexible call use by female Campbell's monkeys varied with the context of calling and reflected an immediate trade-off between signalling identity (better achieved using combined calls involving full arches) and remaining cryptic (using less conspicuous calls).

Interestingly, the trade-off between identity-signalling and crypsis that varied with the immediate context in Campbell's monkeys' contact calls also seemed to apply when comparing the vocal behaviour of Diana and Campbell's monkeys. These two species are closely related and, as a likely result, their vocal repertoires are largely based on a set of homologous acoustic structures. But they adopted distinct socio-ecological strategies that were reflected in their vocal behaviour. Indeed, Diana monkeys are socially more complex, they display an anti-predator strategy mostly based on early predator detection (with no or little need to remain cryptic) and rely strongly on identity-rich but conspicuous arched structures. On the contrary, the vocal communication of Campbell's monkeys, which adopted a cryptic anti-predator strategy and a more low key social life, relies principally on less conspicuous but less identity-rich structures. This opposition was true regarding derived alarm vocalisations as well as call use. Indeed, we highlighted differences in call rates, preferred call types, as well as flexible use of call combination by both species, with likely important consequences on their daily life. This study underlined that future comparative studies would benefit from an approach taking into account not only structural aspects but also factors relating to call's function and flexible use to characterise the vocal communication of animals.

The four studies presented in this thesis follow about two decades of research on the communication in Diana and Campbell's monkeys which provided fine-tuned description of their behaviour and communication, including description of calls' structure, contexts of use and influence on receivers. Such a fine-tuned knowledge was obviously necessary to conduct playback experiments and to formulate hypotheses on the functions and evolution of combinatorial abilities in these animals. Interestingly, the extensive data set available on the communication of these two species and the comparative approach undertaken to characterize

the parallels and differences between their communication systems and human language drew the attention of linguists.

7.2. The vocal behaviour of guenons in linguists' eyes

The detailed data gathered allowed linguists to conduct analyses of the vocal communication in Campbell's and Diana monkeys, using formal linguistic tools. The authors systematically tested the predictions of several models, constructed using methodologies from formal semantics, against the data to determine which model explained the combinatorial patterns observed best.

A first study, based on compositional semantics, used the distinct calling patterns observed in the males of two populations of Campbell's monkeys in Ivory Coast (Taï National Park) and Sierra Leone (Tiwai island) (Schlenker et al., 2014). Indeed, while Hok functions to signal the presence of an eagle in both populations, Krak is used primarily to signal the presence of a leopard in Taï but it has the distribution of a general alarm call on Tiwai (*i.e.* given to a broad range of disturbances including falling trees and eagles) (Arnold, Keenan, Lemasson, & Zuberbühler, 2013; Ouattara, Lemasson, & Zuberbühler, 2009a, 2009b). Importantly, leopards are still present in Taï but disappeared from Tiwai island more than thirty years ago (Stephan & Zuberbühler, 2008). The authors tested two formal models:

The first model posits the following hypotheses: Krak and Hok calls have the same innate meanings in both populations (*i.e.* Krak: general disturbance; Hok: aerial predator). These calls can be further modulated by the addition of an 'oo' suffix which decreases the urgency of the innate meaning (*i.e.* Krak-oo: general and less urgent disturbance; Hok-oo less urgent aerial disturbance). Krak-oo is generated from the innate meaning of Krak in both populations, but in Taï, unsuffixed Krak calls acquired a new meaning: 'leopard-related disturbance'. In other

words, unsuffixed Krak calls have different 'lexical entries' in the two populations but the meaning associated with the Krak root (*i.e.* 'Krak-' part of a Krak-oo call) kept its original meaning in both populations.

The second model proposes an alternative explanation: the innate meaning of Krak and Hok calls are the same in both populations *i.e.* respectively 'urgent general disturbance' and 'urgent aerial disturbance' in both unsuffixed and suffixed calls. But, in this model, the competition between more specific calls and Krak calls leads to the strengthening of the meaning of Krak in a mechanism akin to scalar implicatures. Said differently, Krak has a rather broad meaning (*i.e.* general alarm call) while both Krak-oo (*i.e.* non-urgent danger) and Hok (*i.e.* aerial predator) are more specific. Hence when a male gives Krak calls, a receiver might infer that there is a non-weak and non-aerial disturbance as the call given is Krak but not Krak-oo nor Hok. Hence, the meaning of Krak calls can be strengthened from 'general urgent disturbance' into 'dangerous non-aerial predator'. In Taï the presence of leopards led to the strengthening of the meaning of Krak calls as 'dangerous non-aerial predators' but not in Tiwai where the absence of ground predator prevented the use of strengthened meaning. The authors concluded that the second model was more parsimonious and more likely to describe the associated 'meanings' of calls in the call system of Campbell's monkeys than the first one (Schlenker et al., 2014).

A second study conducted on the alarm calls given by male Campbell's monkeys investigated the "suffixation" system. The authors compared again the predictions made by two distinct hypotheses explaining the presence of an 'oo' unit at the end of less urgent Krak-oo and Hok-oo alarm calls (Kuhn, Keenan, Arnold, & Lemasson, 2014). The first hypothesis was that 'oo' was an actual meaning bearing suffix which was associated with a decrease in urgency. It was tested against the hypothesis that 'oo' did not bear meaning but arised as a side effect of the articulatory process when the urgency of the situation decreased. Indeed, in less urgent

situations Campbell's monkeys use suffixed calls but they also give alarm calls at lower rates and use more acoustically graded forms of their calls than in very urgent contexts (Keenan, Lemasson, & Zuberbühler, 2013; Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010). Firstly, Kuhn and collaborators hypothesized that the 'oo' suffix might serve to slow down the rhythm of calling. Nevertheless, the duration of the 'oo' part in suffixed calls (<0.1 s) was clearly insufficient to explain the variations in call rate (with intercall silence ranging up to 6 seconds). Secondly, they hypothesized that the 'oo' suffix might result in a looser articulation effort by caller leading to a continuation of phonation after the call in more relaxed situations. But, the structural analysis of 'oo' units suggested that, contrarily to Krak and Hok stems that are produced vocally, 'oo' are produced through the nasal cavity. Hence, these structures cannot result from a continuous phonation but rather seem to involve an additional articulatory effort. The authors concluded that the hypothesis posing 'oo' as a correlate of looser or slower articulation in less urgent contexts does not hold. This brings additional support to the hypothesis posing 'oo' as a meaning-bearing suffix (Kuhn et al., 2014).

Finally, a third study involving classical tools of formal linguistic analysis has been conducted on the combinatorial system of female Diana monkeys. The authors analysed the order of emission, the combinatorial structure and the context associated with the distinct call types given by wild females and found non-random patterns. The order of call types given by individuals could be described using linguistic tools to propose rules (defining notably the order and frequency of call types in a sequence and the order and type of calls units that were merged together). The authors proposed two alternative hypotheses to describe the system observed. The first hypothesis proposed that combined calls (*i.e.* HA, LA and RA calls) resulted from the combination of two units that were subsequently used as one call (*i.e.* combined calls hypothesis). On the contrary, the second hypothesis proposed that combined calls consisted in two simple calls given in close succession (*i.e.* maximized adjacency hypothesis). To determine

which hypothesis was the more likely, the authors developed a formal linguistic model for each hypothesis (*e.g.* putative 'rules' of call use describing the observed patterns) and compared them. This work showed that treating these calls as sequences of simple calls failed to account for their distribution in sequences. The most parsimonious model was obtained under the 'combined call hypothesis' (*i.e.* 'combined calls result in the combination of call units and are used as a simple call') as a simple-call analysis (*i.e.* 'combined calls consist in two simple calls given in close succession') would need to be supplemented by phonological complexity in order to account for the data with respect to maximal sequence length and call repetition (Veselinovic, Candiotti, & Lemasson, Under revision).

These studies brought additional support to our findings while adopting very different methodological approaches. Furthermore, they have been exploring a promising area and highlighted the relevance of using general methods of linguistics to get further insights into the communication of animals and its complexity. To our knowledge, no such studies based on formal semantic methodologies have been conducted on the communication systems of animals from other taxa. Yet, several authors found non-random patterns of transitions between the elements of vocal sequences produced by animals (*e.g.* marine mammals: Saulitis, Matkin, & Fay, 2005, bats: Bohn, Schmidt-French, Schwartz, Smotherman, & Pollak, 2009, birds: Dobson & Lemon, 1979; Honda & Okanoya, 1999; Sigler Ficken, Rusch, Taylor, & Powers, 2000). Notably, Kershenbaum and collaborators (2014) analysed the vocal sequences produced by animals from several taxa (*i.e.* killer and pilot whales, rock hyraxes, Bengalese finches, Carolina chickadee, free-tailed bats and orangutans). They tested four Markovian processes (*i.e.* zero, first, second order processes and a hidden Markov model), and two non-markovian processes (renewal process and psychohydraulic model) to determine which one represented best the transition between elements in the sequences recorded. Markovian models are based on the assumption that the probability for an element (*i.e.* here, a call) to occur can be calculated

from the preceding elements in the sequence. The order of the process defines the number of elements taken into account (*e.g.* a first-order Marvok model calculates the probability of emission of a call based on the last call preceding it according to a transition matrix between elements (or a probability of appearance for zero-order markov models; Kakishita, Sasahara, Nishino, Takahasi, & Okanoya, 2009; ten Cate & Okanoya, 2012). The renewal process and psychohydraulic model do not rely on finite memory of the n-th preceding elements: In renewal process models, an element (*e.g.* a call) is repeated for some probabilistically determined number of times before a transition occurs (determined with a pFSA, *i.e.* a probabilistic finite-state automata within which transitions between elements are governed by fixed probabilities). In psychohydraulic models, the probability of occurrence of an element increases with the time since its last utterances and then falls to minimum as soon as it was used (Kershenbaum et al., 2014). This study showed that most of the sequences produced by animals were best described by non-markovian processes rather than simpler pFSA grammars based on Markovian processes. The non-Markovian processes they used have intermediate properties between the pFSA (frequently used to describe call sequences given by animals) and the more complex context-free grammar as found in human languages. Such studies on acoustic patterns of combination are very informative regarding the possible evolution of sequence complexity in animals, and may participate in bridging the gap between human language and animal communication. Nevertheless, in language, combination is relevant only because it is meaningful. Hence, context and relevance to receivers of sequence structure and composition should to be more systematically included in the analysis of animal communication, in particular when one aims to undertake a comparative approach with human language.

7.3. The evolutionary relevance of call combination in primates

Various studies reported capacities of call combination that were meaningful to receivers in primates (see section 1.3 of this thesis). Such mechanisms, as any other complex biological structures and processes, have likely been selected and shaped by natural selection (Darwin, 1872). This implies that they convey somehow an advantage to the individuals in which they occur. We believe that call combination can be advantageous to animals at least in two ways.

7.3.1. The possible benefits of call combination

Firstly, call combination might allow primates to diversify their vocal repertoires and to create new 'messages'. Indeed, primates only possess a limited set of relatively fixed acoustic structures they can produce, but have complex social lives and face distinct predators in more or less urgent situations. As mentioned in the introduction, both predation and social life have been thought of as drivers of the complexity and diversity of signals in animals. The data gathered on combinatorial systems in non-human primates support this view. The diversification of the repertoire can involve 'morphology-like' processes, as exemplified with the suffixation of the 'Krak' stem associated with decreased emergency in male Campbell's monkeys. In addition, calls sequences further allow to increase the diversity of 'messages' conveyed, as for example in putty-nosed monkeys which signal the presence of distinct predators and to trigger group movement using only two distinct call units. Another, maybe more striking, example can be found in black-fronted titi monkeys which use 3 distinct acoustic units (*i.e.* A, B and C) in context-specific call sequences with functions ranging from triggering movement initiation to signalling disturbances and predatory events of various urgency levels (Cäsar, Byrne, Hoppitt, Young, & Zuberbühler, 2012; Cäsar, Byrne, Young, & Zuberbühler, 2012).

Secondly, we believe that call combination may allow primates to produce more informative signals and at the same time to reduce the ambiguity resulting from superimposition of several information within the same call (Green, 1975; Marler, 1975, 1976). Many calls are said to convey cues about relatively stable characteristics of individuals such as identity, body size, social status and affinities (*e.g.* Briefer, 2012; Fichtel, Hammerschmidt, & Jürgens, 2001; Lemasson & Hausberger, 2004; Rendall, 2003; Rendall, Owren, Weerts, & Hienz, 2004; Riede, Bronson, Hatzikirou, & Zuberbühler, 2005). In addition, according to Marler, two important and non-exclusive levels of information are conveyed by animal signals as they comport systematically both a motivational component and a referential one (Marler, Evans, & Hauser, 1992). However, many calls have been selected for a given function and may thus reflect more strongly one component or the other (Marler et al., 1992). As combinatorial processes allow a temporal segregation of the vocal elements, the combination of signals which might have already evolved to ensure a maximal communicative efficiency (e.g. calls with more salient acoustic cues or with a good acoustic adaptation to propagation constraints) is thus susceptible to create richer signals, with increased information content and maximal information transfer.

Some of the data gathered on combinatorial capacities in non-human primates support this hypothesis as they suggested the presence of combined calls that convey complementary cues about caller's imminent behaviour and emotional state (*i.e.* combined calls of wedged-capped capuchins, Robinson, 1984) or involving the concatenation of calls relating to distinct information such as caller's emotional state and identity (*i.e.* H, L or R calls combined with an 'A' call in Diana monkeys Candiotti, Zuberbühler, & Lemasson, 2012; Coye, Zuberbühler, & Lemasson, 2016).

Combinatorial mechanisms were described in calls with varied functions and seem to allow the diversification, refinement or complexification of signals in a very broad range of contexts. The extensive use of combinatorial structures by guenons in the respective cores of males' and

females' communication clearly suggests an essential role of these patterns in their communication. In addition, the presence of such capacities, at various extents, in non-human primate species from distinct groups including Old world monkeys, New world monkeys and apes suggests that combinatorial capacities are probably more widespread than initially though in primates and may count as a valid evolutionary solution to the development of rich, unambiguous communication systems in spite of constraints over acoustic production. Further research will be required to characterize more precisely the occurrences of apparition of combinatorial capacities in the primate lineage as for now, the scarcity of data available prevents us to determine the 'historical path' of this capacity and whether it results from homologies or convergent evolution under similar selective forces in the different groups considered.

7.3.2. A cognitive ground for combinatorial structures?

The work of Seyfarth, Cheney and collaborators (Bergman, Beehner, Cheney, & Seyfarth, 2003; Cheney & Seyfarth, 1999; Cheney, Seyfarth, & Silk, 1995; Seyfarth, Cheney, & Bergman, 2005), showed that non-human primates possess a developed social cognition involving a hierarchically structured representational knowledge of social relationships, governed by rules and involving causal inference as a likely result of their complex social life. In addition, some studies based on experimental tasks suggested that non-human primates possess, to some extent, capacities to handle combinatorial and sequential structures as well as organisational rules in a broader sense.

Firstly, the capacity of non-human primates to learn sequential lists of items has been demonstrated with both visual and auditory elements (Terrace, Son, & Brannon, 2003; Wright, Santiago, Sands, Kendrick, & Cook, 1985). Secondly, some primates were able to compute the

probability with which syllables and letters occured in a particular order and to group adjacent syllables in word-like units as they could discriminate between words and non-words composed of the same sounds or letters after training (Grainger, Dufau, Montant, Ziegler, & Fagot, 2012; Hauser, Newport, & Aslin, 2001; Ziegler et al., 2013). Furthermore, a few studies also demonstrated that monkeys seemed able to acquire quickly (*i.e.* after 20 to 30 minutes of exposure) general 'rules' of structuring as they could acquire simple pFSA grammar (see this chapter section 2) (Fitch & Hauser, 2004) and identify non-adjacent dependencies between syllables and shorter sound segments (*i.e.* vowels) (Newport, Hauser, Spaepen, & Aslin, 2004). Finally, experiments with language-trained apes suggested that these animals were able to acquire a productive and receptive vocabulary and to respond correctly to word order (Savage-Rumbaugh, Rumbaugh, & McDonald, 1986; Sevcik & Savage-Rumbaugh, 1994). Apes also demonstrated advanced capacities in terms of production. Notably, gestures were given more frequently in a given order than the reverse (*e.g.* 'me Nim' more than 'Nim me') (Seidenberg & Petitto, 1979) and some gestures were spontaneously combined into more complex structures (*e.g.* 'water bird', by Washoe) by signing apes (Gardner & Gardner, 1975). Furthermore, Kanzi, the bonobo seemed able to acquire grammatical rules involving generalization of the rule to categories of signals (Patterson, 1978). However results concerning the production capacities and acquisition of very complex syntactic structures remained controversial. Chimpanzees and gorillas did not seem to actually acquire rules for utterance structure and produced long and ungrammatical sequences involving numerous repetitions (Seidenberg & Petitto, 1979). In line with this, if cotton top tamarins acquired easily pFSA grammars of the AB^N form, they failed to acquire recursive structures of the form A^NB^N. (but see Gentner, Fenn, Margoliash, & Nusbaum, 2006; Marcus, 2006 and Petkov & Wilson, 2012 for views challenging this result and discussing the protocol).

Globally, the presence –at least to a certain extent- of such abilities in fairly distant primate species suggests that a basic cognitive ground to handle combinatorial processes might be widespread in non-human primates. However, further studies will be required to get a more comprehensive view of the capacities and cognitive limitations of primates when it comes to dealing with complex rule-governed structures.

The work reviewed and conducted during this thesis confirms the relevance of the primate model to get insights into the evolution of combinatorial features and to draw parallels with possible mechanisms leading to the emergence of language. As mentioned in section 1.1.3 of the introduction, studies investigating natural call combinations in non-primate animals generally tackle this question with a distinct approach. However, some studies investigated the presence of combinatorial processes by accounting for the relevance to receivers of distinct combinatorial structures in a way similar to the work described in primates. These studies suggest that combinatorial capacities may have appeared on several distinct occasions in the animal kingdom, under the pressure of analogous selective forces.

7.4. Linguistic-like abilities in non-primate species

With a structure akin to that of section 1.3 of this thesis, we propose to describe sequentially the distinct type of combinatorial processes highlighted in non-primate animals.

7.4.1. Phonology-like structures

As a reminder, a phoneme is a meaningless sound unit which, when added or used to replace another sound unit in a word, modifies the initial word into a new one. Hence, we proposed that a phonology-like process would require: (1) a combination involving vocal unit(s) that are

not associated to any given context (environmental, behavioural or emotional); (2) that this combination (or the addition of a meaningless unit to an existing call) creates a call consistently associated with a context that does not depend on any prior contextual association of the elements that constitute it (as opposed to morphology-like combination).

As previously mentioned, no examples of phonology-like structures have been described in non-human primates. But several animal species display a more plastic vocal production than primates, and often combine apparently meaningless sounds into larger structures (notably songbirds). These animals would thus be logical 'candidates' for the study of phonology-like structures. Nevertheless in most cases, changes of one meaningless note (or set of notes) in sequence organisation could not be proven to relate to changes in the function or perceived 'meaning' of a sequence by receivers (Berwick, Okanoya, Beckers, & Bolhuis, 2011; Engesser, Crane, Savage, Russell, & Townsend, 2015).

To our knowledge, only one demonstration of phonological-like combination exists in animal. It was described and experimentally validated in chestnut crowned babblers (*Pomatostomus ruficeps*), a species of Australian passerines (Engesser et al., 2015). These birds live in groups within which all the adults cooperate to breed the nestlings of the dominant pair (Russell, Portelli, Russell, & Barclay, 2010). They possess a complex communication system involving at least 13 discrete call types, composed of one to more than 5 notes (Crane, Savage, & Russell, In press). In particular, chestnut crowned babblers possess two calls (*i.e.* flight and prompt call) based on distinct combination of two meaningless elements ('A' and 'B'). The flight call is an "AB" structure given during flight, and the prompt call is a "BAB" structure emitted during nestling provisioning. The authors combined analyses of each element's acoustic structure, natural observations and playback experiments to wild subjects and proposed that these calls constitute an example of phonemic contrast as the addition or deletion of a B element to an AB structure differentiates flight and prompt calls to receivers. Notably, they obtained similar

reactions to natural and artificially recombined flight calls (*i.e.* consisting of the 'AB' part of a prompt call) as well as similar reactions to natural and artificially recombined prompt calls (*i.e.* consisting of a 'B' element added to a flight call). Furthermore, the diffusion of single 'B' units and 'CAB' artificial stimuli (with 'C' being a call element naturally given in combination with other notes by chestnut babblers) triggered surprised reactions very different from those obtained by the broadcast of flight or prompt calls, thus ruling out a possible 'priming effect' of a 'B' element as well as the possible role of a three-element structure in the reactions obtained (Engesser et al., 2015). Now, further research will be needed to determine whether the other call pairs (*i.e.* two calls given in distinct contexts and that differ only by one element) of the vocal repertoire of chestnut babblers also involve a similar process.

7.4.2. Morphology-like combinations:

As proposed in the introduction, combinatorial processes showing analogous traits with morphology in animals would consist in the junction of two vocal units from which receivers can extract information, into a more complex structure which information content depends on: (1) the units merged together and their respective information content; and (2) rules for units combination (*i.e.* systematic order of combination and eventual consistent alteration of the information conveyed by signal).

Here again, an example of morphology-like combination has been reported in a species of cooperatively breeding passerines, the pied babbler (*Turdoides bicolor*) (Engesser, Ridley, & Townsend, 2016). These non-singing birds possess a vocal repertoire counting 17 discrete calls (Golabek, 2010). Notably, pied babbers give an alert call with a broadband structure in response to sudden but low-urgency threats and a more tonal, repetitive, recruitment calls to recruit group members to a new location in quiet context (*e.g.* roosting or foraging). In addition, pied babblers combine sequentially alert and recruitment calls into 'mobbing sequences' when

encountering and mobbing at predators. After verifying the context-specificity of production of alert calls, recruitment calls and mobbing sequences using natural observations, the authors conducted a playback experiment to verify the combinatorial structure of the mobbing sequence and to determine whether pied babblers extract the meaning of the sequence in a compositional way (Engesser et al., 2016). They tested subjects' reaction to the broadcast of natural alert calls, recruitment calls and mobbing sequences. Furthermore, they also used artificially recombined mobbing sequences, built with alert and recruitment calls initially given apart from each other in their respective contexts of emission, and 'artificial' recruitment calls, *i.e.* the 'recruitment segment' of a mobbing sequence. The results confirmed the context-specificity of the three types of stimuli and their relevance to receivers. Importantly, there was no difference between subjects' reaction to natural and artificial stimuli, and no impact of the origin of the recruitment element on observed reactions, which further confirmed the combinatorial nature of mobbing sequences. An additional control playback was performed using mobbing sequences in which the alert element was replaced by another broadband call naturally given by pied babblers (*i.e.* the foraging chuck call). Contrarily to mobbing sequences, these stimuli did not trigger increased attentiveness towards the sound source nor mobbing behaviours in receivers. These results confirmed that neither a 'two-element' structure nor the association of any call before a recruitment call (*i.e.* 'priming effect') could explain the responses given to mobbing sequences and brought additional support to the hypothesis of a compositional structure of the mobbing sequences in pied babblers. Importantly, receivers' reaction to mobbing sequences exceeded the sum of reactions to their components (*i.e.* higher attentiveness and quicker approach) suggesting that, in this case, the combination of two elements did not simply led to an addition of their meanings but related to a 'new' meaning *i.e.* 'mobbing a predator'.

Another case of fully documented morphology-like combination of call units into combined calls has been reported in meerkats (Manser et al., 2014). These animals give two distinct alarm calls to signal predators on the ground (*i.e.* the terrestrial alarm calls) (Manser, 2001) and when an animal is moving and passing by on the ground or flying close to the ground (*i.e.* the animal moving call) (Manser, Hollén, Steinert, Dewas, & Townsend, In Prep.). These calls can be given separately in the corresponding contexts or merged together into a complex call when a terrestrial predator is moving (Manser et al., 2014).

Other species have been subject to investigation and seem to possess similar systems although further work will be required to characterise them completely. Dwarf mongooses (*Helogale parvula*) possess a terrestrial alarm call and an aerial alarm, given respectively to terrestrial and aerial threats. These calls can be further combined sequentially into a larger structure (*i.e.* aerial alarm followed by terrestrial alarm). The latter being given mostly after that the group was alerted of the presence of an aerial threats with aerial alarm calls. Although an acoustic analysis revealed small variations in the structure of the 'terrestrial' component of the combined call, receivers gave similar responses to natural combined calls and to artificially recombined calls (created by merging an aerial and a terrestrial alarm calls initially given separately). The results from the playback strongly confirms the presence of combinatorial processes in dwarf mongoose alarm calls (Collier, Radford, Bickel, Manser, & Townsend, n.d.) and now further research will be required to clarify the exact functions of the combined call.

Interestingly, another example of call combination was reported in a third member of the *Herpestidae* family: the banded mongoose. Acoustic analyses and behavioural observations of wild banded mongooses showed that they possess a combinatorial system in which a contact call composed of two segments is given in three distinct contexts: when the caller is digging, searching and moving (Jansen, Cant, & Manser, 2012). The first segment relates strongly to caller's identity and remains identical in the three contexts. The second segment varies

gradually as a function of caller's activity: when the caller is digging the segment is absent (or very short), it's duration increases when the caller is searching, and reaches its maximal value (together with more pronounced harmonics) when the caller is moving. A playback experiment confirmed that between-caller variations in the identity segment were relevant to receivers as pups could discriminate between the (digging) calls of their escorting adults and those of other adults (Müller & Manser, 2008). In addition, banded mongoose possess a second layer of combinatorial structures that may relate to some sort of syntactic-like ability. Indeed, they can give call sequences involving a contact call (of the 'foraging' type) and another element, separated by a short silence. Such sequences were given in three distinct contexts: when the caller was leading the group, encountering water (or moisture) or when it was lost. The number of elements added and their acoustic structure varied consistently with the context. However, the exact nature of the combinatorial system described here remains unclear as both phonological and morphological process could explain the patterns described.Now, further experimental testing will be required to determine the nature of information changes associated with the various call segments involved (Collier, Bickel, Schaik, Manser, & Townsend, 2014).

7.4.3. Syntactic-like sequences

Several examples of long and or complex call sequences composed of various units have been reported in animal from various taxa (*e.g.* songbirds: Adret-Hausberger, 1982; Beckers, Bolhuis, Okanoya, & Berwick, 2012; Catchpole, 1987, marine mammals : Au et al., 2006; Payne & McVay, 1971, terrestrial mammals: Hammerschmidt, Radyushkin, Ehrenreich, & Fischer, 2009; Holy & Guo, 2005; Kanwal, Matsumura, Ohlemiller, & Suga, 1994; Kershenbaum, Ilany, Blaustein, & Geffen, 2012). Yet, only a few might fit the definitions we proposed for syntactic-like abilities in animals. As previously, we will distinguish between 'lexical syntax' and 'phonological syntax' and will mention here call sequences. In both

'lexical' and 'phonological' syntax, the fundamental feature lies in the relationship between changes of information content and changes of sequence's structure. While most cases of 'animal syntax' reported so far involve complex sequences with a clear functional role (*e.g.* protection of territorial borders and mate attraction), changes in the type of calls involved or their order were frequent and did not relate with changes in call's function and contextual use (Bremond, 1968; Gammon & Altizer, 2011; Honda & Okanoya, 1999; Kroodsma, 1977; Riesch, Ford, & Thomsen, 2008), as confirmed by receivers' reaction (European robin: Bremond, 1968; yellow-naped amazons: Dahlin & Wright, 2012, wren: Holland, Dabelsteen, & Paris, 2000). In those cases, variations in call sequences are important as well, and they notably seem to provide information about caller's group or geographic origin (*e.g.* dialects) while signals' main function is maintained (Baptista & King, 1980; Bitterbaum & Baptista, 1979; Emlen, 1972; Harris & Lemon, 1972; Slater, Clements, & Goodfellow, 1984; Snowdon & Hausberger, 1997, p. 136). Such cases, as exemplified by Collier and colleagues (Collier et al., 2014) in their analysis of winter wren's song, may be described rather as 'phonetic patterning' than phonological syntax.

The chick-a-dee calls of birds in the parid family are highly variable and complex structures involving the combination of various call units (*i.e.* A, B, C, D and E notes). Call composition and rhythm seems to vary according to the context and to relate to the urgency of danger or to the type of predator in various species (Courter & Ritchison, 2010; Templeton, Greene, & Davis, 2005) although the variations were different depending on the species considered. For example, while the degree of threat and predator size related to the number of D notes per unit of time in the chickadee calls of tufted titmice (Courter & Ritchison, 2010), they related to the number of D notes (which increased with threat) and their duration (which decreased with threat) in black-capped and Carolina chickadees (Soard & Ritchison, 2009; Templeton et al., 2005). In addition, in this latter species, other changes relate to contextual events, notably, the

proportion of C units increased in sequences given when the caller was flying while the proportion of A notes increased in sequences given after the detection of an aerial threat (Freeberg, 2008). Importantly,changes in note composition of the sequence triggered distinct reactions from receivers (Freeberg & Lucas, 2002). Nevertheless, the exact sequence of notes involved seemed very variable and the changes reported by authors systematically consisted of variation in the proportion of a given call type. Now, further testing will be necessary to determine whether those systems rely on morphology-like or phonology-like processes. In particular, and before drawing stronger conclusions, it will be necessary to determine whether the notes bear some intrinsic message.

Suzuki and collaborators (2016) recently conducted a playback experiment to investigate the combinatorial nature of the chickadee calls in Japanese great tits (*Parus major*). In predatory contexts, these animals combine three notes (A, B and C) together in various ways, the most frequent being an A-B-C call which playback triggers an increased visual scanning by receivers. In parallel, Japanese great tits give sequences of D units which apparently function to recruit other individuals, for example when an individual is visiting its nest and recruit its mate. They can further combine these two structures into a ABC-$D_{repeated}$ sequence that seems to possess a compound message as its playback triggers both an increased scanning (as an 'ABC' call) and approach by receivers (as a D sequence). The authors further showed that in addition to possess a compound 'message', the order in which units were associated was important since the broadcast of recombined '$D_{repeated}$-ABC sequences only rarely triggered the same responses in receivers. The authors concluded that the calling system of Japanese great tits involves a compositional syntax. Nevertheless, future studies will be necessary to clarify the system underlying the structure of the first part ('chicka') as it can be composed of various combinations of A, B and C notes (*e.g.* AC or BC) which function or precise contextual correlates (if any) remain unclear.

Finally, other examples of complex call sequences in animal may involve systematic combination of call units in a way meaningful to receivers although the relevance of changes to receiver's or the contextual correlates of sequence's structure are still lacking (*e.g.* Norwegian killer whales: Shapiro, Tyack, & Seneff, 2011). This is notably the case in rock hyraxes which song seems to involve meaningless units that are never given alone. The organisation and composition of these songs seem to relate to body weight, size, social status, hormonal state and geographical location (Kershenbaum et al., 2012; Koren & Geffen, 2009).

Similarly, some species of bat possess complex songs which apparently follow structural rules and which composition is susceptible to relate to contextual factors or to caller's internal state (Bohn, Schmidt-French, Ma, & Pollak, 2008; Kanwal et al., 1994). In particular, authors hypothesized that the presence of 'buzz' units in the song of free-tailed bats might relate to caller's willingness to aggressively defend its territory. But the lack of experimental evidence of the relevance of this pattern and variations (in order and call composition) to receivers prevents us to draw stronger conclusions (Bohn et al., 2009). Interestingly, the song of mustached bats obeys structural rules and an experiment showed that the broadcast of sequences with an altered organisation (*e.g.* reversed order) affected the pattern of neuronal response in the auditory cortex of subjects (Esser, Condon, Suga, & Kanwal, 1997). However if this experiment suggested that subjects perceived changes in sequence's organisation, the lack of information about the behaviour associated with the emission or perception of distinct songs prevents us again to conclude firmly.

Globally, evidence for functionally meaningful combinatorial capacities in a broad range of vertebrates strongly suggests that they likely possess an adaptive value and emerged in several occasions during the evolution of animals. Interestingly, the presence of combined calls in both species with discrete (*e.g.* chestnut-crowned babblers) and graded (*e.g.* banded mongoose) call repertoires suggests that these process may be advantageous to species with distinct

communication systems. Importantly, two common traits seem redundant: firstly, to our knowledge, no examples of natural functionally meaningful call combination have been highlighted in species with high levels of acoustic plasticity, supporting the hypothesis that combinatorial processes might play an important role to overcome production constraints. Secondly, all the species displaying combinatorial systems live in group. This observation is consistent with the comparative analysis conducted by Manser and collaborators (Jansen, 2013, p. 201; Manser et al., 2014) which suggested a positive relationship between the social complexity and, among other things, the presence and complexity of combinatorial structures in *Herpestidaes*.

Animal communication and complex combinatorial structures have been under the scope of scientists for several decades. Yet, we believe that the findings recently obtained from various domains and interdisciplinary research, together with the development of highly performing tools for data collection, handling and analysis (in regards of acoustic, physiological and behavioural aspects) pave the way to a promising field of studies susceptible to bring important insights into the evolution of language and of animal communication in general.

7.5. Future prospects

Human language is a unique communication system. Yet its complexity suggests that it did not appear *de novo* but most likely built over pre-existing capacities through an evolutionary path driven by the laws of natural selection. Comparative studies have already proven their relevance to shed light on the processes underlying animal communication and its evolution outside and within the primate lineage. Now, further research will be necessary to get a deeper understanding of the combinatorial systems described in animals as they might help us identify

some pieces of the puzzle of communication. The systems described in this thesis still present grey areas which clarification would be valuable.

Future prospects on the communication of Diana monkeys

Firstly, we recently described arched structures, given in alarm contexts (*i.e.* Alk and W calls). The exact function and information conveyed by these calls remain unclear. **Notably, we do not know whether they relate to distinct contexts, to caller's emotional state or both, and their potential to signal caller's identity also remains unclear.** We believe that an in-depth analysis of the kinetic of females' response to stressful events, and an analysis of caller recognition (using artificial neural networks and playback tests on wild subjects) might allow us to get insights into these questions.

On a more experimental area, further playback experiments of both natural and artificial stimuli would be required **to verify subject's reaction to natural calls and test the impact of call manipulation** as slight changes in call structure remain a possibility. To this end, we could for instance broadcast natural LA and RA calls from group members, as well as 'manipulated' versions of these calls (*i.e.* created by cutting the call units before merging them together again).

In addition, it would be useful to **test subjects' reaction to the playback of reverse-order calls** (*e.g.* artificial 'AL' or 'AR' calls instead of 'LA' and 'RA' calls). This would allow us to verify whether the order of call units is important or if their juxtaposition is sufficient, and would bring further insights into the perception that females have of combined calls' organization.

Future prospects on the communication of Campbell's monkeys

The communication of female Campbell's monkey has been described more extensively in both alarm (Ouattara, Zuberbühler, N'goran, Gombert, & Lemasson, 2009) and social contexts (*e.g.* Lemasson, Gautier, & Hausberger, 2005; Lemasson & Hausberger, 2011; Lemasson, Gandon, & Hausberger, 2010; Lemasson & Hausberger, 2004). Yet the combinatorial aspect of their vocal repertoire would require further investigation.

Firstly, **testing experimentally the combinatorial structure of females' combined calls** (*i.e.* CH calls), involving both natural and artificially recombined stimuli would be a required step to bring further evidence on the use of combinatorial processes by these animals.

Secondly, as in Diana monkeys we could **test subject's reaction to the broadcast of reverse combination** (*i.e.* with the arched structure preceding the low-pitched quaver).

Similarly, in males, further experimental evidence will be required to improve our knowledge of their combinatorial system. We hypothesized that the suffixation mechanism described in Krak and Krak-oo calls could be found more generally in the other call types, notably Hok/Hok-oo calls (and Wak/Wak-oo on Tiwai island). But this hypothesis was based on observational data (and supported by "formal semantic" analysis). Now, it remains to be tested. To this end, we firstly suggest to **replicate the experiment presented in Chapter 3 using Hok and Hok-oo calls** to verify the suffixation mechanism in this call pair as well. Secondly, it will be necessary to verify that the 'oo' suffix added is the same across call types, to ensure the homogeneity of the suffixation process**.** We propose **to test the 'transferability' of the 'oo' suffix between Krak-oo and Hok-oo calls using playback experiments** involving natural (Hok-oo and Krak-oo) calls as well as artificial calls created with suffixes taken from a suffixed call of another type (*i.e.* Hok-oo calls with the 'oo' from a Krak-oo call).

Finally, the presence of captive male and female Campbell's monkeys at the Station Biologique de Paimpont offers the possibility **to test their ability to acquire and generalize more or less abstract syntactic rules.** We believe that studies based on habituation/dishabituation paradigms and operant conditioning technics would be particularly relevant in this species that displays complex combinatorial mechanisms in both sexes. It would notably be interesting **to compare the performances of males and females** that are similarly exposed to combined structures but differ in their use as this might allow us to hypothesize on the relative importance of production and exposition in the development of the ability to handle combinatorial rules.

Future prospects in other species

Firstly, we believe that it will be necessary **to pursue the efforts to clarify and homogenize the terminology** used to describe combinatorial capacities of animals that parallel linguistic structures. Eventually, it would be useful to develop a new lexicon specifically designed to refer to such structures that would better correspond to the systems described.

Secondly, and in a more empirical aspect, it seems **important to pursue the work on the combinatorial systems already identified.** This includes species in which promising studies were already conducted but for which further research will be needed to get a more precise view of the complete systems (*e.g.* apes: Crockford & Boesch, 2005; Hedwig, Mundry, Robbins, & Boesch, 2015). This also includes species whose repertoires may contain additional combinatorial processes that have not been formally tested yet (*e.g.* other call pairs of chestnut crowned babblers), in order to get a better understanding of the distribution of combinatorial processes in the repertoire of these animals.

It will also be necessary **to determine whether other vocal communication systems involve combinatorial processes, particularly in species that are phylogenetically distant from**

primates. In this regard, bats and birds (notably species with discrete repertoires based on a limited number of distinct units) seem to be particularly relevant candidates. Such developments in the study of combinatorial capacities in animals would offer a remarkable framework to investigate the evolution of these abilities in species from various taxa, living in distinct habitats or with different social systems.

The ability to handle combinatorial and sequential structures as well as organisational rules have already been demonstrated in non-primate animals. For instance, starlings could acquire rules of recursive patterning after intensive training (Gentner et al., 2006), while cotton-top tamarins had failed (although differences in the protocol prevent more substantial comparisons; Marcus, 2006). Captive bottlenose dolphins and language-trained parrots displayed the ability to understand languages (artificial or natural ones), including abilities of syntactic processing and generalization to syntactically and lexically novel sentences (Herman, Richards, & Wolz, 1984; Pepperberg, 1981; Pepperberg & Pepperberg, 2009, p. 20). Finally some language-trained grey parrots combined spontaneously morphemes and phonemes and learned to associate them with new objects, suggesting that they attended the segmental structure of their utterances (*i.e.* involving subparts combined together) and the possibility to create new, distinct, utterances by recombining segments (Pepperberg, 2007, 2010). Hence, we believe that **there is an urgent need for additional studies providing complementary views into the capacities of animals to handle combinatorial structures and rules and to generalize acquired patterns.** This could help us clarifying which cognitive processes may (or may not) be required to achieve such tasks.

Finally, as previously suggested, it would be interesting **to determine whether the capacity to handle combinatorial structures finds correlates in the natural communication of animals.** For instance: do species with vocal systems that naturally involve combinatorial mechanisms perform better than species that do not (Saffran et al., 2008)? This last aspect

might be particularly promising and future studies investigating the presence of correlates between social complexity, combinatorial abilities and cognition might bring insights into the possible evolutionary paths adopted by our ancestors.

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CURRICULUM VITAE

Curriculum Vitae

Camille Coye

Education

09/2012 - Present	Doctoral programme under joint supervision of St Andrews University (UK) and University of Rennes 1 (France). Co-directors: Pr Klaus Zuberbühler and Pr Alban Lemasson.
10/2013	Official Degree **"Design and application of experimental procedures on animals"**, (National Veterinary School 'Oniris' - Nantes), required in France to submit experimental protocols to Ethic committees and conduct experiments as Principal Investigator.
2011-2012	Second year of Master's Degree: "Human and animal behaviour", Rennes 1 University. With honours, Rank: 3/23 *Main topics:* Ethology, Neurobiology, Communication. **Research internship:** Six-months research internship, Ethos research unit (Rennes). Director: Pr Catherine Blois-Heulin. **Research topic:** Adaptation to receiver's attention and gestural communication in captive Campbell's monkeys.
2010-2011	First year of Master's Degree: "Human and animal behaviour", Rennes 1 University. With honours, Rank: 1/90. *Main topics:* Ethology, Ecology, Population dynamics. **Research internship:** Three-months research internship, EcoBio and Ethos Research Units (Rennes) Co-directors: Dr Eric Petit and Pr Aban Lemasson. **Research topic:** Relationship between genetic proximity and social relationships in wild Diana monkeys.
2007-2011	Bachelor's degree on Human and Animal Physiology, Blaise Pascal University. With honours, Rank: 1/47. *Main topics:* Physiology, Biochemistry, Genetics and Immunology.

Management and administrative responsibilities

09/2014 - 08/2016	PhD Students representative in the Laboratory Council of Ethos Research Unit (UMR CNRS 6552)
2013 - 2015	Camp manager of the "Taï Monkey Project" field site (Ivory Coast) during the missions. Management of the work of eight field assistants, logistics, safety and accountings for the project.

Teaching

08/2015 - Present **Temporary lecturer at the University of Rennes 1** (Teaching and Research activity)
Teaching activities (290h): Practical courses in Ethology and Neurosciences to students in Bachelor's and Master's degree in Biology, Ethology and Psychology. Topics: Behavioural observation (birds, rodents) on audio-taped recordings and living animals, introduction to data analysi, human behaviour (laterality, galvanic skin response and audiometry).

2012 **Teaching assistant at the University of Rennes 1 during the doctorate (64h):** Practical courses in Neuro-ethology: "Nervous system and Behaviour" (First year of Bachelor's degree in Biology) and "Neurosciences of Behaviour" (Third year of Bachelor's degree in Psychology). Topics: foraging behaviour of Eurasian oystercatchers, human behaviour (response time to visual and audio stimuli, topographic learning).

2008-2009 Private lessons in Biology, Physics and Chemistry to high school students in scientific cursus.

Additional courses attended

03/2015 Workshop in statistics (14h): **'Experimental Design and analysis of variance'** at St Andrews University (UK), with the "Biomathematics and Statistics Scotland" Laboratory.

02/2015 Workshop in statistics (14h): **'Regression and curve fitting'** at St Andrews University (UK), with the "Biomathematics and Statistics Scotland" Laboratory.

02/2014 Workshop on teaching theory (8h): **'Learning strategies and management of students' motivation'** at Rennes 1 University, with the Centre of engineering and multimedia resources.

Publications

Coye, C., Zuberbühler, K., & Lemasson, A. (2016). Morphologically structured vocalizations in female Diana monkeys. *Animal Behaviour*, *115*, 97–105.

Bouchet, H., Coye C., & Alban Lemasson, H. (2016). Le langage est-il le propre de l'homme? Apports des études sur les primates non humains. *Tétralogiques, 21, 87-133.*

Coye, C., Ouattara, K., Zuberbühler, K., & Lemasson, A. (2015). Suffixation influences receivers' behaviour in non-human primates. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1807), 20150265.

Candiotti, A., Coye, C., Ouattara, K., Petit, E. J., Vallet, D., Zuberbühler, K., & Lemasson, A. (2015). Female Bonds and Kinship in Forest Guenons. *International Journal of Primatology*, 36(2), 332-352.

International Conference Contributions

10/2015 Conference of the Francilien Institute of Ethology, Villetaneuse, France. Invited speaker. Oral presentation : **'Capacités combinatoires dans la communication vocale de cercopithèques'.**

08/2015 6th Meeting of the European Federation for Primatology (EFP), Roma, Italy. Invited to the symposium 'Vocal communication'. Oral presentation: **'Suffixation in non-human primates: meaningful sound combinations in free-ranging guenons'**.

08/2014 25th Congress of the International Primatological Society (IPS), in Hanoi, Vietnam. Oral presentation: **'Suffixation influences receiver's behaviour in non-human primates'**.

ANNEXES

Tétralogiques, n°21, 2016, pp. 87-133

LE LANGAGE EST-IL LE PROPRE DE L'HOMME ? APPORTS DES ETUDES SUR LES PRIMATES NON HUMAINS

Hélène BOUCHET[*, a], Camille COYE[b], Alban LEMASSON[b]

Résumé

Le langage, vu comme une entité complexe, est considéré comme le propre de l'homme. En revanche, si l'on choisit de décomposer le langage en une somme de propriétés (complémentaires mais) distinctes, il devient possible d'établir des parallèles avec l'animal. Les primates non humains présentent un intérêt comparatif tout particulier de par leur proximité phylogénétique avec l'homme. En nous appuyant sur des études éthologiques récentes, nous tenterons d'évaluer dans quelle mesure certaines propriétés du langage (e.g. contrôle vocal moteur, combinaisons syntaxiques, plasticité vocale, règles conversationnelles) ne sont finalement pas le propre de l'homme. Nous examinerons quels sont les parallèles pouvant être établis entre homme et singes, et quelles sont les limites à ces comparaisons.

Introduction

La question de l'appartenance du langage à l'homme est, depuis l'antiquité, régulièrement sujet à controverses. Aristote considérait déjà, dans sa *Politique* (env. -340 av. J-C.), l'homme comme un « animal politique parlant » chez qui la voix est signifiante. La philosophie s'est longtemps emparée de cette question, avec, par exemple, Descartes qui dans son *Discours de la méthode* (1637) défend l'idée que les animaux peuvent « proférer des paroles » sans pour autant « parler… c'est-à-dire en témoignant qu'ils pensent ce qu'ils disent. ». Pour éviter les « querelles stériles et les thèses farfelues », la société de linguistique de Paris indique en 1865 dans son règlement ne plus souhaiter recevoir aucune communication concernant l'origine du langage. En parallèle, la biologie continue à s'intéresser à cette question de l'évolution du langage, avec en premier lieu, Darwin qui, dans son livre sur les origines de l'homme (*The descent of man, and selection in relation to sex*, 1871) affirme que « l'homme n'est pas le seul animal qui puisse user d'un langage pour

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exprimer ce qui se passe dans son esprit, et comprendre plus ou moins ce qui est dit par un autre ». Il cite notamment l'exemple des singes du Paraguay qui « murmurent un ensemble de six mots distincts quand ils sont dans un état d'excitation, tout en provoquant chez leurs congénères des émotions similaires ». Aujourd'hui le débat est transdisciplinaire, opposant des courants de pensée prônant, pour les discontinuistes, une différence d'ordre qualitative [1–3] et, pour les continuistes, une différence d'ordre quantitative [4–8] entre le langage humain et la communication vocale animale ; certains auteurs ont récemment suggéré un positionnement intermédiaire, mêlant ces deux courants à première vue antagonistes [9].

Le langage est un comportement social [10, 11], et ce dès l'enfance [12] : l'acte de communication consiste en une interaction sociale entre un individu émetteur/locuteur et un ou plusieurs individus receveurs/ récepteurs par le biais d'un échange de signaux [13, 14]. Pour Dunbar [15], le langage est pour l'homme un instrument de cohésion sociale, au même titre que le toilettage chez les singes qui est bien moins lié à des questions d'hygiène que de cimentage de lien social. Ainsi, au cours de l'évolution des primates, lorsqu'il y a eu élargissement de la taille du groupe social, l'instrument « toilettage manuel » se serait révélé peu efficace, laissant place à l'échange de signaux vocaux et progressivement au langage. Chez les macaques japonais, l'idée que l'échange vocal puisse être vu comme un « toilettage vocal, à distance » vient justement d'être démontrée, ces deux comportements se distribuant de manière identique au sein du réseau social : les femelles qui s'épouillent le plus lorsqu'elles sont à proximité sont également celles qui échangent vocalement le plus lorsqu'elles sont distantes [16]. Ainsi l'éthologie, qui s'intéresse à l'étude des comportements animaux et humains et notamment à la communication spontanée et aux interactions entre les membres d'un groupe chez différentes espèces animales plus ou moins sociales, peut apporter une contribution significative au débat.

Le langage consiste en un système organisé de signaux arbitraires et de structures dont l'agencement est régi par des règles, utilisé à des fins de communication [17]. Si l'on considère le langage comme une entité complexe caractérisée par des propriétés telles que la générativité (capacité de générer un nombre infini de messages à partir d'un nombre fini d'éléments), la récursivité (construction syntaxique pouvant se répéter un nombre indéfini de fois à partir du résultat qu'elle produit), la fonction symbolique (évocation de situations ou d'objets en se servant de signes ou symboles) et les capacités de déplacement (capacité de référer à des évènements ou choses éloignés dans le temps et l'espace), il semble être le propre de l'homme [18, 19] ; un tel niveau de complexité n'ayant pas, à ce jour, été observé dans les productions vocales

spontanées chez l'animal. En revanche, si l'on décompose le langage en une somme de propriétés (complémentaires mais) distinctes (comme la sémantique, la syntaxe, l'apprentissage social, la plasticité acoustique, les règles conversationnelles), observées dans toutes les langues du monde, il devient alors possible de tenter d'établir des parallèles avec l'animal [5, 6, 8, 9, 20]. Tandis que certains traits demeureront propres à l'homme, d'autres caractéristiques essentielles du langage pourront se révéler être partagées avec l'animal et, selon les propriétés, par des espèces plus ou moins éloignées phylogénétiquement de l'homme. Cette approche s'interroge sur l'existence d'un réel fossé qualitatif entre langage humain et communication animale, et recherche les possibilités de le combler en identifiant des similarités, identités ou différences partielles selon les cas, entre l'homme et l'animal. C'est cette approche que nous utiliserons dans cet article.

Nous passerons alors en revue un certain nombre de propriétés du langage et tenterons d'évaluer dans quelle mesure ces caractéristiques sont finalement, ou non, le propre de l'homme. Nous nous intéresserons ainsi aux capacités de contrôle moteur de la production vocale, aux composantes émotionnelle/référentielle/identitaire des messages, aux propriétés combinatoires des productions vocales, au développement vocal chez le jeune, aux capacités de plasticité vocale sous influences sociales chez l'adulte, ainsi qu'à l'ajustement à l'audience et aux règles temporelles et sociales des interactions vocales. Nous nous appuierons sur la littérature récente concernant la communication vocale chez les primates non humains qui présentent un intérêt comparatif tout particulier de par leur proximité phylogénétique avec l'homme.

1 Contrôle moteur de la production vocale

Chez l'homme, le langage oral repose en premier lieu sur sa capacité à contrôler sa voix de manière volontaire, que ce soit en termes d'émission (choisir de parler ou de rester silencieux) ou en termes de modulation de la structure acoustique (articulation, prosodie, capacité d'imitation). Cette faculté s'appuie sur des prédispositions anatomiques (e.g. descente du larynx), cérébrales (e.g. aire de Broca) et neuronales favorables [21, 22]. L'homme présente notamment un circuit neuronal direct entre le cortex moteur et le larynx lui permettant un contrôle affiné de son appareil phonatoire [23].

Au sein de l'ordre des primates, les capacités de contrôle vocal observées chez l'homme sont inégalées, les singes n'auraient qu'un contrôle très limité sur leurs productions vocales [24, 25]. On a longtemps pensé que ces inégalités reposaient sur des différences fondamentales du point de vue de l'anatomie du tractus vocal [26]. Or de

récents travaux de modélisation ont montré que les singes possèdent les prédispositions anatomiques de base requises pour le contrôle articulatoire et laryngé [27, 28]. Cela suggère que les différences inter-spécifiques en termes de flexibilité vocale ont plus à voir avec le degré de contrôle neuronal dont dispose chaque espèce qu'avec des divergences anatomiques.

Les émissions vocales des singes ont longtemps été considérées comme essentiellement automatiques car liées quasi-exclusivement au niveau d'excitation de l'émetteur, avec une production associée à des structures cérébrales subcorticales et notamment au système limbique [29–31]. Cependant, il est important de souligner que nombre de ces anciennes études ont, pour des raisons techniques, été menées chez des sujets anesthésiés ou restreints dans leurs mouvements, un contexte critiquable d'un point de vue biologique et social [32]. En outre, il est intéressant de noter que, si certaines études ont permis de provoquer la production de cris via la stimulation de régions cérébrales profondes chez les singes, les vocalisations obtenues étaient exclusivement des cris d'alarme ou de détresse ([33, 34] mais voir [35] pour la seule exception). Aucune étude n'a permis l'expression de la totalité du répertoire d'une espèce.

De récentes études de conditionnement opérant ont relancé le débat sur la capacité de contrôle vocal des primates non humains, vraisemblablement sous-estimée jusqu'alors. En effet, des singes se sont révélés capables d'interrompre brutalement leur vocalisation à la diffusion d'un bruit blanc [36, 37], d'apprendre à vocaliser sur commande en réponse à un signe de la main de l'expérimentateur humain [38], ou d'être conditionnés à vocaliser sur présentation d'un item alimentaire [39] ou d'un stimulus visuel [40]. Des expériences de manipulation du bruit de fond ont révélé que les singes sont également capables de moduler la structure acoustique de leur cri (amplitude, durée) de façon à optimiser les chances de diffusion de leur signal dans un milieu bruyant [41, 42] (remarque : pour des exemples de modulation dans le domaine fréquentiel, sous l'influence de facteurs sociaux, voir les phénomènes de convergence vocale décrits §6 et §7). De plus, les bases neurobiologiques de cette aptitude au contrôle vocal chez les primates non humains ont pu être identifiées [39, 40, 43]. Ces études ont mis en lumière le rôle joué par le cortex prémoteur et le cortex préfrontal, des aires cérébrales également impliquées dans la production du langage chez l'homme (i.e. homologues de l'aire de Broca). En outre, d'après ces mêmes études, l'activation des aires cérébrales n'est pas identique selon le contexte de production vocale. Certaines émissions vocales, notamment celles émises spontanément sans raison apparente, sont plutôt automatiques, alors que d'autres,

notamment celles impliquées dans un échange vocal social, sont plutôt volontaires [43]. D'un point de vue neuronal, le contexte d'interaction sociale semble donc plus propice à la plasticité vocale. Nous verrons, au cours de cette revue, que les exemples de variabilité sous influences sociales sont effectivement nombreux.

En résumé, le contrôle vocal chez les primates non humains a longtemps été considéré comme quasi inexistant, pour des raisons anatomiques d'une part, et parce que les émissions vocales des singes étaient vues comme de simples manifestations réflexes de l'état émotionnel de l'émetteur (associées à des structures cérébrales sub-corticales) d'autre part. Or de récentes études ont révélé que les différences homme-singes reposeraient finalement plus sur des capacités inégales de contrôle neuronal que sur des divergences anatomiques, même si des différences qualitatives subsistent à ce niveau (e.g. mobilité de la langue [44]). Des études expérimentales ont permis d'observer un certain degré de contrôle vocal chez les singes, que ce soit en termes d'émission (choisir de crier ou non selon le contexte) ou en termes de modulation de la structure acoustique. Des bases neurobiologiques communes (implication du cortex prémoteur et du cortex préfrontal) au sein de l'ordre des primates ont même pu être identifiées, notamment s'agissant des vocalisations émises en contexte social. On ne peut donc plus parler de réelle discontinuité à ce niveau, même si des différences importantes subsistent. Par exemple, en dépit de l'existence de relevés anecdotiques d'imitation de signaux humains voisés (e.g. le chimpanzé Viki, après un entraînement intensif, aurait été capable de prononcer 4 mots [45]) ou non-voisés (e.g. plusieurs orangs-outans captifs produisent des sifflements par imitation de leurs soigneurs humains [46]) par des grand-singes, les grandes capacités d'imitation de l'homme demeurent inégalées.

2 Composantes émotionnelle/référentielle/identitaire des messages

Chez l'homme, la voix et la façon de parler sont porteuses d'informations relatives à l'état émotionnel du locuteur, encodées par la prosodie (i.e. vitesse d'élocution et variations de tonalité) [47–49], qui sont d'une grande importance pour les relations sociales, en lien notamment avec l'empathie. Elles sont également porteuses d'informations sur son identité. Il est intéressant de noter que la quantité d'indices identitaires présents dans le discours varie selon la situation, notamment en fonction du nombre d'auditeurs-cibles (communication de masse *versus* conversation en tête-à-tête) et de la composition de l'audience (étrangers *versus* individus familiers) : le discours sera plus riche en informations identitaires dans un contexte intime, mais plus

neutre dans un contexte public [50]. Mais le cœur du langage humain est sa sémantique, soit l'association de signaux arbitraires pour référer à des éléments pourvus de sens, qui permet à l'homme de communiquer sur tous les sujets, qu'ils soient concrets ou abstraits (capacité d'abstraction), et qu'ils soient proches ou éloignés dans le temps et l'espace (capacité de déplacement) [19].

Classiquement, les vocalisations animales ont été considérées avant tout comme des reflets acoustiques de changements de l'état interne (émotionnel) de l'émetteur [30, 51]. En effet, chez les singes comme chez l'homme, des variations de tonalité, de durée ou de rythme encodent des variations de l'état émotionnel [52]. Ainsi, chez les saïmiris, le degré d'aversion est encodé dans la structure acoustique des cris (amplitude, fréquence, ratio signal sur bruit) [35]. Chez les mones de Campbell, lorsque le niveau de danger augmente (i.e. prédateur entendu à distance *versu*s prédateur détecté visuellement à proximité, ce qui constitue un danger imminent), les mâles émettent leurs cris d'alarme plus rapidement [53], tandis que lorsque le groupe a subi une séparation prolongée, les cris de contact des femelles au moment des retrouvailles sont plus longs et plus aigus que la normale [54].

D'autres auteurs ont défendu l'idée d'un codage acoustique d'informations référentielles relatives à un stimulus extérieur tel qu'une source de nourriture (quantité, qualité ; e.g. macaques [55], tamarins [56], chimpanzés [57]) ou un risque de prédation (type de prédateur notamment terrestre *versus* aérien, degré d'imminence du danger ; e.g. vervets [58], cercopithèques Diane [59], mones de Campbell [60, 61], capucins [62]), ou encore d'informations relatives au succès (éjaculation) ou non d'un acte de copulation (e.g. macaques [63]). Pour mettre en évidence ce codage d'informations référentielles, il est possible de conduire des expériences dites « de repasse » qui consistent en l'utilisation de cris pré-enregistrés, déclenchés par des évènements extérieurs distincts identifiés (e.g. la présence d'un prédateur), pour une diffusion ultérieure (i.e. « repasse ») en l'absence du stimulus initial (i.e. le prédateur). De telles expériences permettent de confirmer que les cris seuls suffisent pour provoquer des réactions comportementales très spécifiques et identiques à celles observées dans le contexte d'origine (i.e. risque de prédation). Par exemple, la repasse de cris d'alarme signalant un prédateur induit les mêmes réactions que la présence du prédateur : lever la tête ou fuir vers le haut pour un prédateur terrestre, et l'opposé pour un prédateur aérien [64–67]. Cette composante référentielle des vocalisations animales s'apparente au caractère sémantique des mots dans le langage humain, et il a également été suggéré que les vocalisations puissent être associées à des représentations mentales chez les receveurs [65, 68] même si

l'hypothèse d'un simple apprentissage associatif ne peut être exclue à l'heure actuelle. Il est important de remarquer que la composante référentielle des signaux n'a pu être mise en évidence que pour un nombre restreint de types de cris parmi l'ensemble formant le répertoire vocal des primates non humains, en l'occurrence les cris alimentaires, les cris d'alarme, ou encore les cris de copulation, mais pas les cris émis en contexte d'interaction affiliative par exemple.

Finalement, un modèle dual réconciliant ces deux courants de pensée a été proposé, considérant que les cris des primates non humains pouvaient présenter à la fois une composante émotionnelle et une composante référentielle [69], comme c'est le cas chez l'homme. Mais les études de ces 20 dernières années ont révélé qu'une troisième composante, la composante identitaire, pouvait s'avérer particulièrement développée, notamment dans les cris dont les composantes émotionnelle et référentielle sont de moindre importance. Cet encodage d'informations identitaires cruciales leur confère alors une fonction de « badge social ». L'appartenance de l'émetteur à une espèce [70], une population [71], un groupe social [72, 73], une lignée génétique [74, 75], un réseau social [76], mais aussi son sexe, son âge, sa taille corporelle [77], son statut hiérarchique [78], sans oublier son identité individuelle [79,80] sont autant d'informations pouvant être encodées dans les cris des singes. Au sein d'un groupe, ces informations vont par exemple pouvoir être utilisées par les receveurs pour choisir d'intervenir, ou non, dans un conflit opposant deux congénères dont les cris auront indiqué la lignée, le sexe, le rang hiérarchique, l'identité individuelle, etc... Ainsi, un mâle babouin ne va s'approcher d'un conflit que s'il entretient des liens d'amitié forts avec la femelle allaitante agressée, qu'il n'a pu apprendre à reconnaître vocalement qu'après sa migration au sein du groupe à l'âge adulte [81]. Par ailleurs, les babouins sont plus attentifs à un conflit suggérant un renversement de hiérarchie entre deux lignées, qu'à un conflit intra-lignée [7]. L'encodage d'informations identitaires dans les cris est important dans nombre de contextes, mais c'est le cas plus particulièrement pour ceux émis dans le cadre des interactions sociales (et qui ne sont donc pas des cris dits référentiels) où l'identité des acteurs est un paramètre essentiel. Cette idée a donné naissance à une hypothèse selon laquelle le degré d'encodage de l'identité dans les cris varierait au sein du répertoire vocal, en lien avec la fonction sociale de chaque type de cri [82–85]. Les cris impliqués dans la médiation des relations intra-groupe et dirigés vers un partenaire social particulier (par exemple les cris affiliatifs) seraient sujets à des pressions (sociales) de sélection en faveur d'un degré important de variabilité. Cela permettrait notamment l'encodage d'informations relatives à l'identité de l'émetteur (variabilité inter-individuelle), à son état émotionnel ou encore à ses « intentions » en termes de stratégies sociales (variabilité intra-

individuelle). Au contraire, les cris émis dans un contexte moins social et dirigés vers l'ensemble du groupe (par exemple les cris d'alarmes) seraient sujets à des pressions de sélection en faveur d'une plus grande stéréotypie permettant d'éviter tout risque de confusion du signal. Cette hypothèse a été validée récemment grâce à des études évaluant le degré de variabilité acoustique dans tout ou partie du répertoire vocal chez plusieurs espèces. En effet, les cris affiliatifs sont ceux qui présentent le degré de variabilité des paramètres acoustiques le plus élevé et qui encodent l'identité de la manière la plus fiable [82, 84, 86–88]. En revanche, chez ces mêmes espèces, les cris agonistiques, les cris d'alarme, ou les cris liés à l'alimentation ont une structure comparativement plus stéréotypée avec peu de variabilité intra- ou inter-individuelle [82, 84, 86]. Un parallèle intéressant peut être fait avec ce que l'on observe chez l'homme dont le degré de personnalisation du discours varie en fonction de l'audience visée [50].

Pour illustrer l'existence simultanée de ces trois composantes (référentielle, émotionnelle, identitaire) dans les messages vocaux d'une même espèce de primate, on peut citer l'exemple des mones de Campbell. Chez cette espèce, les mâles produisent six types de cris forts qu'ils émettent en séquences dont la composition varie en fonction du type de danger [60, 89] : chute d'un arbre, détection d'un groupe voisin, détection d'un prédateur avec précision possible du type (léopard, aigle…). En outre, la rythmicité de ces séquences [53], ainsi que la structure acoustique même des cris (paramètres temporels et fréquentiels) [20], varient en fonction du degré d'imminence du danger (prédateur détecté acoustiquement *versus* visuellement), reflétant donc l'état émotionnel de l'émetteur. Enfin, des informations identitaires sont encodées dans la structure acoustique de certains cris (paramètres fréquentiels) [20] ainsi que dans l'organisation temporelle de certaines séquences [53].

En conclusion, tandis que des parallèles homme-singes peuvent aisément être établis lorsque l'on s'intéresse aux caractères émotionnel (avec notamment le lien prosodie-émotions) et identitaire des messages (avec notamment le degré de personnalisation du discours en fonction du public visé), c'est concernant la composante référentielle que les différences les plus importantes subsistent. Les signaux des animaux réfèrent à des éléments présents dans leur environnement à l'instant *t*. Leurs messages présentent donc un caractère sémantique, mais de par leur manque de détachement par rapport au contexte immédiat, ils ne remplissent pas de fonction symbolique et n'apportent pas la preuve d'une faculté de déplacement, par opposition au langage humain [19]. Enfin, même s'il est difficile d'affirmer aujourd'hui que les singes possèdent une représentation mentale du contenu référentiel des cris

qu'ils entendent, il semblerait qu'ils ne réagissent pas sur la base d'un simple processus d'apprentissage associatif. C'est donc du point de vue des processus cognitifs sous-tendant la sémanticité que des investigations supplémentaires demeurent nécessaires avant de pouvoir établir la limite de l'analogie homme-singes.

3 Propriétés combinatoires des productions vocales

Une des caractéristiques essentielle du langage est le principe de double-articulation (ou dualité d'assemblage) qui implique une structure combinatoire à deux niveaux, régie par de nombreuses règles grammaticales : le premier niveau concerne l'assemblage d'unités sans valeur sémantique (les phonèmes) en éléments porteurs de sens (les morphèmes et mots), et le second la combinaison de ces unités sémantiques au sein de structures plus importantes (les phrases) dont le sens dépend de règles syntaxiques [19, 90]. Cette caractéristique clé du langage humain est à la base de notre capacité à générer une infinité de message à partir d'un nombre fini d'éléments.

Traditionnellement, les études chez les primates non humains se sont focalisées sur l'identification des différents types de cris émis par une espèce. Or, dans l'optique d'une approche comparative avec l'homme sur la question de la double-articulation, plusieurs auteurs ont récemment souligné l'intérêt de privilégier une analyse multi-niveaux de la structure organisationnelle du répertoire vocal des primates non humains [91–93]. Aussi, des études récentes se sont intéressées à l'existence de systèmes combinatoires chez les singes, et ont révélé l'existence de correspondances avec la structure impliquant plusieurs niveaux (phonèmes – morphèmes – mots – phrases) communément admise chez l'homme. Plusieurs espèces de primates non humains possèdent en effet des systèmes communicatifs impliquant à minima trois niveaux : différents cris (i.e. signaux ayant une structure distincte et une fonction propre, associés à un ou des contextes d'émission particuliers) peuvent être émis tels quels (« cris simples »), ou bien concaténés (avec des unités vocales n'étant jamais émises isolément, ou avec d'autres cris) pour former des « cris complexes » dont la fonction dépend des parties qui les composent ; enfin, les cris (« simples » ou « complexes ») peuvent être combinés en « séquences vocales » (i.e. série de cris émise par un même individu) dont la signification varie en fonction des cris qui les composent, l'ordre dans lequel ils sont émis et/ou leur rythme d'émission [93]. Le répertoire vocal des singes apparaît alors comme un système plus flexible, avec des combinaisons fonctionnelles optionnelles, mais prédictibles, de structures acoustiques.

Pour faciliter la comparaison homme-singes concernant les propriétés combinatoires de leurs productions vocales, nous avons décidé d'emprunter la terminologie linguistique utilisée classiquement dans l'étude de la morphologie [94] pour décrire des phénomènes qui nous semblent comparables ; toutes précautions gardées sur les limites de cette analogie. Nous utiliserons ainsi le terme « d'affixation » lorsqu'un « cri complexe » est formé par ajout d'un affixe à un radical ; un « affixe » référant à une unité acoustique n'apparaissant que comme sous-partie d'une vocalisation, et n'ayant pas de fonction propre prise indépendamment (par opposition au « radical » qui possède une fonction propre lorsqu'il est émis seul). Nous qualifierons de « préfixe » tout affixe se rattachant à l'avant d'un radical, et de « suffixe » tout affixe se rattachant à l'arrière de celui-ci. Enfin, nous parlerons de « syntaxe » lorsqu'il s'agira de décrire les règles de combinaison d'éléments fonctionnels en séquences plus complexes.

De récentes études se sont ainsi intéressées à un premier niveau d'organisation des émissions vocales des primates non humains : la façon dont des unités vocales sont combinées afin de former des cris complexes. Cela a permis de mettre en évidence qu'à partir de quelques unités discrètes, les singes sont capables d'émettre une grande variété de signaux. On trouve un exemple de suffixation chez les mangabés à collier dont quatre types de cris simples (émis en contexte alimentaire ou social) peuvent être combinés à une unité 'Uh' (jamais émise seule par ailleurs). L'utilisation de ce suffixe est fonction du contexte social : les cris comprenant un 'Uh' sont émis plus souvent lors d'échanges vocaux impliquant de multiples partenaires que lors d'émissions vocales isolées [95]. Un autre exemple, remarquable, est celui de la mone de Campbell. Les mâles produisent des cris d'alarme spécifiques au type de danger détecté : les cris 'Krak' signalent un danger au sol (i.e. un léopard, ou un autre danger urgent au sol dans les régions où ce prédateur n'est plus présent ; voir [96] pour une analyse linguistique dialectale du phénomène se basant sur les implicatures scalaires), alors que les cris 'Hok' signalent la détection d'un aigle [60]. Ils peuvent également combiner ces cris simples à un suffixe unique 'oo' (cette unité 'oo' n'est jamais émise seule) pour former les cris complexes 'Krak-oo' et 'Hok-oo'. Ces derniers sont émis dans un contexte plus large de perturbation, moins urgente, respectivement au sol et dans la canopée. Ainsi, l'affixation d'une unité 'oo' permet d'élargir le sens du message porté par les cris simples 'Krak' et 'Hok', et d'en atténuer l'urgence [60]. La valeur sémantique des 'Krak' et des 'Hok' ainsi que des cris 'Krak' suffixés ('Krak-oo') a été confirmée expérimentalement. Lorsqu'ils entendent des repasses de cris 'Krak' ou 'Hok', les cercopithèques Diane qui vivent en sympatrie (i.e. co-existent dans un même habitat et interagissent fréquemment) avec les mones de

Campbell se comportent comme si le prédateur (terrestre ou aérien) avait été détecté [65], et ils répondent plus fortement aux cris non-suffixés 'Krak' (léopard) qu'aux cris suffixés 'Krak-oo' (danger non-spécifié) [97]. Il a en outre été prouvé que la moindre urgence associée aux cris suffixés n'est pas la conséquence d'un simple ralentissement de la séquence lié à la contrainte d'émission de ces unités additionnelles [98]. De plus, des analyses structurales [98], ainsi que des expériences de repasses de cris artificiellement recombinés [97], ont démontré que les cris complexes consistent bien en la combinaison linéaire d'une racine et d'un suffixe. La linéarité des contextes associés aux cris simples et suffixés (i.e. 'Krak-' = sol ; 'Hok-' = canopée) et l'utilisation d'un unique suffixe pour les deux combinaisons suggèrent une possible règle communicative : « '-oo' atténue l'urgence ». Toutefois, les capacités cognitives impliquées dans ce phénomène restent méconnues et d'autres études évaluant la capacité des animaux à généraliser cette règle sont nécessaires avant de pousser plus avant la comparaison homme-singes, et de conclure sur l'existence d'une « proto-grammaire ».

Plusieurs auteurs ont également décrit des productions vocales impliquant non plus la combinaison d'une racine avec un affixe, mais la combinaison de deux cris simples ensemble pour former un cri complexe dont la signification dépend de ses composants (e.g. chimpanzés [99]). C'est par exemple le cas des cercopithèques Diane, une espèce proche de la mone de Campbell, chez qui les femelles peuvent émettre quatre cris simples : 'H', 'L', 'R' et 'A'. Les trois premiers ('H', 'L', 'R') sont émis en fonction de la valence émotionnelle du contexte social, respectivement dans un contexte positif, neutre et négatif. Le quatrième ('A') est émis dans des contextes variés et comporte deux sous-types dont la structure encode l'identité de l'émetteur plus (sous-type 'Af') ou moins (sous-type 'Ab') fortement. Ces cris peuvent être combinés, non-aléatoirement, en six cris complexes comportant une partie contextuelle ('H', 'L' ou 'R') et une partie identitaire ('A') [100]. Les différents cris complexes (i.e. 'HAf', 'HAb', 'LAf', 'LAb', 'RAf' et 'RAb') sont utilisés dans des contextes correspondant aux sous-unités qui les composent, suggérant l'existence d'une addition des messages vocaux. Récemment, une expérience de repasse de stimuli artificiels (i.e. recombinaison pertinente de cris recréée à partir de cris émis indépendamment) a démontré que les receveurs perçoivent les différences acoustiques et adaptent leur réaction en fonction du type de cri complexe diffusé [101], confirmant ainsi la pertinence biologique des combinaisons de cris chez les primates non humains. Un système analogue de combinaisons de cris a été mis en évidence chez les femelles mones de Campbell qui produisent des cris complexes dont la première partie encode l'état

émotionnel de l'émetteur (un paradigme expérimental de séparation-réunion a mis en évidence une augmentation de la tonalité et de la durée consécutive à un stress social plus important [54]) et la seconde partie, caractérisée par une modulation de fréquence en forme d'arche, encode son identité (une expérience de repasse a confirmé la capacité de reconnaissance individuelle par les récepteurs sur la base du pattern de cette arche [102]).

Enfin, un niveau d'organisation supérieur s'est révélé riche en informations contextuelles, celui des séquences de cris. Ainsi, les bonobos émettent leurs cris alimentaires en séquences dont la composition, en termes de types de cris, varie en fonction du type de nourriture [103], et cette information est décodée avec succès par les receveurs [104]. Un autre exemple remarquable, mentionné précédemment, est celui des séquences de cris d'alarmes (2 à 40 cris émis à la suite) des mâles mones de Campbell. Leur analyse a révélé un système de combinaisons complexe, reposant sur des associations et des transitions (i.e. ordre de succession des cris) non-aléatoires entre les six différents types de cris ('Boom', 'Krak', 'Krak-oo', 'Hok', 'Hok-oo' et 'Wak-oo'). Ce système encode des informations aussi diverses que la nature et l'imminence du danger, le type de prédateur et l'activité du mâle [89]. Par exemple, une série de cris 'Boom' est une incitation au rassemblement et au déplacement du groupe, tandis qu'une série composée de cris 'Krak-oo' est émise lorsqu'un prédateur est détecté. Mais la combinaison des deux (soit une séquence composée de cris 'Boom' suivis de cris 'Krak-oo') est émise dans un contexte radicalement différent, suite à la chute d'un arbre. Et lorsqu'un groupe voisin est détecté, des cris 'Hok-oo' sont ajoutés à l'intérieur de la séquence « chute d'arbre » qui porte alors encore un nouveau message, cette fois-ci territorial. Par ailleurs, l'ajout de cris 'Krak' à une séquence « alerte générale au prédateur » (série de 'Krak-oo') sert à spécifier le type de prédateur détecté (léopard). En outre, il est apparu que l'organisation de ces séquences vocales est prévisible puisque les informations cruciales sont données dès le début de la série de cris [89]. Par exemple, les cris 'Boom' produits dans un contexte de non-prédation sont émis en premier. Les cris simples ('Krak' et 'Hok') informant sur le type de prédateur détecté sont également émis avant les cris suffixés (« alerte générale ») au sein d'une séquence. D'ailleurs, des repasses de séquences vocales enregistrées dans un contexte de détection d'un prédateur, auxquelles des cris 'Boom' avaient été artificiellement ajoutés, n'ont pas provoqué de réaction anti-prédatrice chez les individus récepteurs [66]. Enfin, le rythme d'émission des cris au sein de la séquence s'est également avéré être porteur d'informations. Le débit d'émission des cris 'Krak' et 'Krak-oo' augmente en fonction de l'imminence du danger (léopard détecté visuellement *versus*

acoustiquement), tandis que le rythme d'émission des 'Hok' augmente lorsque le mâle s'apprête à contre-attaquer l'aigle détecté [53]. Les exemples indiquant que l'émission de cris en séquences permet d'affiner le message ou bien de créer de nouveaux messages se sont multipliés ces dernières années [62, 105–109].

L'analyse de la structure des productions vocales des primates non humains a permis de mettre en évidence plusieurs niveaux d'organisation révélant un système complexe de combinaisons, perçues et interprétées par les receveurs de manière appropriée. Des parallèles avec les aspects sémantiques morphologiques et syntactiques du langage peuvent être envisagés [91, 110]. On observe notamment des analogies entre cris simples référentiels et mots simples (i.e. composés d'un seul morphème), entre affixes associés à une modification systématique du message (e.g. '-oo' des mâles mones de Campbell) et affixes lexicaux, entre combinaisons de cris/affixes et mots complexes (ou composés selon les items combinés), et enfin entre séquences et phrases. Toutefois, ces analogies restent préliminaires et d'autres études seront nécessaires afin de confirmer ou infirmer ces propositions. En outre, le niveau phonétique chez l'animal n'a pas été étudié, ce qui limite les comparaisons avec le principe de dualité d'assemblage caractéristique du langage humain [91]. Quoiqu'il en soit, les primates non humains ne présentent de toute évidence pas les propriétés de générativité et de récursivité observées dans les productions vocales chez l'homme : tous les types de cris ne sont pas impliqués dans des combinaisons, les processus combinatoires engagés sont simples comparés aux règles grammaticales du langage, et la taille restreinte et le caractère fermé du répertoire vocal des singes limite les possibilités de combinaisons qui sont infinies chez l'homme. Si nous possédons déjà certaines clés quant aux mécanismes et capacités cognitives impliqués dans la production et la perception des vocalisations (contrôle volontaire de la production et intentionnalité, représentation mentale et inférences sur l'environnement), de nombreuses questions restent en suspens afin de clarifier les limites des parallèles pouvant être tracées entre langage humain et communication animale. La question des mécanismes cognitifs sous-tendant les combinaisons chez les singes (i.e. règles de combinaisons réelles, ou apprentissage de motifs complexes seulement associés à différents contextes) reste notamment ouverte.

4 Développement vocal chez le jeune : déterminisme génétique *versus* apprentissage social

Chez l'homme, une phase de babillage précède l'apparition des premiers mots chez l'enfant [6, 111]. Le développement des différents aspects du langage se fait sous l'influence de tuteurs sociaux

(notamment les parents) qui vont guider l'apprentissage par l'enfant des aspects prosodiques [6, 112], du contenu sémantique [113], du contexte d'émission des vocalisations (aspects pragmatiques) [114–116], ou encore des règles conversationnelles [6, 117]. Les quelques cas célèbres « d'enfants sauvages » ont confirmé que, chez l'homme, le manque d'expérience auditive et sociale crée un retard de développement de la production vocale : l'apprentissage du langage au-delà de la période sensible est limité, voire impossible [118–120]. En outre, l'homme fait preuve de plasticité vocale tout au long de sa vie (i.e. apprentissage vocal ouvert) : il peut perpétuellement apprendre de nouveaux mots, une nouvelle langue et ses nouveaux phonèmes, ou encore imiter de nouvelles voix.

Le développement de la communication vocale chez les singes est, depuis les études pionnières des années 1970-1980, considéré comme étant sous l'emprise d'un fort déterminisme génétique [24, 121, 122], par opposition au langage humain dont l'acquisition nécessite un apprentissage social complexe. Des expériences d'isolement social ou d'assourdissement à la naissance [123–125] ont montré que, même en l'absence de tous stimuli sociaux ou auditifs, les vocalisations des primates non humains apparaissaient dès la naissance comme structurellement comparables à celles des adultes et variaient peu par la suite. Ces expériences méritent cependant d'être relativisées car le juvénile ne peut jamais être totalement privé d'expérience sociale (notamment au stade prénatal). Par ailleurs, des expériences d'hybridation et d'adoption croisée [126–128] ont montré que les individus hybrides produisaient des vocalisations dont la structure était intermédiaire entre les deux espèces parentes, laissant supposer un fort déterminisme génétique. Cependant, le fait que ces expériences aient été réalisées avec des espèces phylogénétiquement proches empêche de le conclure avec certitude [127, 128]. En effet, de larges comparaisons interspécifiques ont mis en évidence qu'une forte proximité phylogénétique se traduisait par une plus grande ressemblance vocale au sein de plusieurs taxons (e.g. cercopithèques forestiers : *Cercopithecus* sp. [70], gibbons : *Hylobates* sp. [129]). Enfin, il est à noter que des expériences similaires apportent parfois des résultats contradictoires [130], possiblement imputables aux progrès des techniques de mesure acoustique depuis la fin des années 1980 [85, 122]. Des réplications récentes [131, 132] des expériences d'élevage en isolement social des années 1970 [124] ont révélé un certain degré de variabilité acoustique structurale au cours du développement qui serait seulement en partie expliqué par des changements morpho-anatomiques maturationnels. En outre, il s'est avéré que tous les types de cris n'apparaissaient pas sous leur forme adulte dès la naissance : certains présentent un degré de changement plus important au cours du développement [133, 134]. Un

cas exceptionnel de flexibilité vocale a été rapporté chez deux espèces de ouistitis [135–137] dont les juvéniles présentent un phénomène de « babillage », comparable à ce que l'on peut observer chez les enfants humains [10]. A la naissance, les jeunes ouistitis produisent de longues séquences de cris de structures variées. Au cours du développement, les séquences émises sont de plus en plus courtes, et la structure des cris des juvéniles évolue vers des formes adultes, notamment grâce aux feedback de leurs aînés [137]. Enfin, une étude récente sur les duos mère-fille chez les gibbons a mis en évidence un degré de flexibilité acoustique dans le chant du jeune qui va au-delà de simples changements maturationnels [138]. Au cours du développement, les femelles immatures produisent des chants qui sont de plus en plus ressemblants acoustiquement et de plus en plus synchrones avec ceux de leur mère ; cette dernière jouant un rôle de tuteur facilitant l'apprentissage en produisant des chants stéréotypés.

Maintenant, si l'on s'intéresse à un autre aspect de la communication qui est, non pas la production abordée précédemment (i.e. émission de cris caractérisés par un ensemble de paramètres acoustiques), mais l'utilisation des vocalisations (i.e. fréquence et spécificité du contexte d'émission), il existe chez les primates non humains un certain nombre de preuves d'apprentissage social du contexte d'émission approprié [122, 139, 140]. Ainsi, au cours du développement, on observe un affinement progressif du contexte d'utilisation des différents types de cris [141–144]. Par exemple, les jeunes vervets apprennent progressivement à émettre le cri d'alarme spécifique à la détection d'un aigle martial à bon escient : d'abord émis envers tout objet volant (y compris une feuille d'arbre) par les plus jeunes, puis envers toutes les espèces d'oiseaux par les juvéniles, il est enfin préférentiellement émis envers les espèces de rapaces et surtout l'aigle martial par les adultes [58, 145]. L'expérience et l'observation du comportement des adultes joueraient un rôle primordial dans cet apprentissage. En outre, les adultes participent parfois activement à l'apprentissage de l'utilisation des cris par les juvéniles [146]. Chez les tamarins, l'émission de cris alimentaires par les adultes associée à des transferts de nourriture (de l'adulte vers le jeune) permettrait au juvénile d'apprendre non seulement quels aliments sont convenables, mais aussi quelles vocalisations sont appropriées en contexte d'alimentation [147]. Par ailleurs, les preuves d'un apprentissage social des règles d'interaction régissant les échanges vocaux se multiplient : les jeunes singes apprennent au fil du temps à répondre de manière appropriée, avec le bon délai et au bon moment, aux vocalisations de leurs congénères (e.g. mones de Campbell [148], macaques [6, 149], ouistitis [150]). En ne répondant qu'aux vocalisations émises dans le respect des règles d'échange, les parents

joueraient là encore un rôle de tuteur dans l'apprentissage des jeunes [150].

Enfin, à l'âge adulte, quelques études mettant en évidence des capacités d'innovation vocale sont également venues remettre en cause l'idée que le système d'apprentissage chez les singes était strictement fermé (i.e. absence de plasticité vocale tout au long de la vie). Tout d'abord deux exemples anecdotiques chez des chimpanzés [151] et des orangs-outangs [152] qui se sont mis à produire de nouveaux signaux en captivité, respectivement destinés à attirer l'attention des humains ('extended grunt' et 'raspberry') ou produits par imitation de ces derniers (sifflement). Chez les mones de Campbell aussi des différences entre populations captives et sauvages ont été rapportées. Tandis que les femelles sauvages produisent trois types de cris liés à des types distincts de danger (dangers divers autres que prédation, détection d'un aigle, détection d'un léopard) [61], les femelles captives ne produisent aucun des deux cris d'alarme liés aux prédateurs mais elles émettent le cri associé aux dangers divers ainsi qu'un second cri, innovant, à l'approche d'humains « inquiétants » (e.g. vétérinaire, personne non familière) [153]. La captivité constituerait ainsi une nouvelle niche écologique propice au développement de capacités vocales innovantes [154].

Ces études récentes sont donc venues remettre en question la présupposée totale fixité du répertoire vocal des primates non humains. Le fait que le développement du répertoire vocal des singes soit soumis à un fort déterminisme génétique reste indiscutable, mais au niveau individuel, il existe un certain degré de flexibilité dans la production vocale chez le juvénile qui perdure à l'âge adulte. Les preuves de l'importance de l'expérience et des influences sociales sur le développement de l'utilisation vocale (i.e. émission d'un cri dans un contexte approprié) sont quant à elles nombreuses chez les singes, et présentent de nombreux points communs avec le développement du langage chez l'enfant.

5 Plasticité vocale et « identité sociale » chez l'adulte

Chez l'homme, la voix et la façon de parler encodent de nombreuses informations relatives à l'identité sociale et personnelle du locuteur. Ainsi, l'origine géographique transparaît dans le langage humain sous la forme d'accents ou de dialectes régionaux (i.e. variations liées à la distance spatiale), tandis que l'appartenance à une entité sociale est reflétée par l'existence de dialectes sociaux (i.e. variations liées à la distance sociale) et par un phénomène de convergence vocale (i.e. les amis ou les apparentés font correspondre leur façon de parler) [10, 155–157]. En outre, l'identité personnelle du locuteur, soit des paramètres

tels que son sexe, son statut ou sa classe sociale, donne lieu à des variations en termes de phonation, de vocabulaire ou encore de style [156, 158, 159]. Les influences sociales sur la plasticité vocale observée chez l'homme sont donc diverses et variées, et elles affectent le langage à tous les niveaux, de la phonation à la syntaxe en passant par le champ lexical.

Au cours des recherches menées ces 15 dernières années, les facteurs sociaux se sont révélés source, chez les primates non humains, d'un degré de variabilité vocale chez l'adulte jusqu'alors sous-estimé. Ainsi, l'appartenance de l'émetteur à une population donnée se reflète dans la structure acoustique de certains types de cris (i.e. « dialecte phonologique ») [71–73, 160–162], voire dans la composition de son répertoire vocal (présence/absence de types de cris ou de messages encodés, i.e. « dialecte sémantique ») [96, 163]. Les études ont prouvé que les dialectes ne sont pas liés à une divergence génétique entre les populations [71, 161], et que les caractéristiques de l'habitat occupé ne suffisent pas non plus à expliquer les différences inter-groupes observées [72, 73, 160, 161, 164, 165]. Pour expliquer la présence, à un moment donné, de structures acoustiques similaires dans le répertoire de congénères appartenant à une même entité, l'hypothèse d'un phénomène d'apprentissage social semble souvent la plus plausible. Une étude longitudinale chez les macaques a d'ailleurs révélé que les différences inter-populations n'apparaissaient chez les juvéniles qu'après l'âge de 6 ou 7 mois [71]. De plus, une étude portant sur des chimpanzés captifs a mis en évidence une modification de la structure des cris alimentaires lors d'un changement de groupe, cette convergence vocale n'apparaissant qu'après la mise en place de liens sociaux affiliatifs forts entre les individus [166]. Ces résultats soutiennent l'idée que l'expérience sociale joue un rôle prépondérant dans l'acquisition des dialectes.

Au sein même d'un groupe social, des différences interindividuelles liées à l'appartenance de l'émetteur à un réseau affinitaire peut également transparaître dans ses vocalisations. Ce phénomène de partage vocal a notamment été mis en évidence chez les mones de Campbell : les femelles ayant des liens sociaux privilégiés émettent les mêmes variantes de cris de contact (caractérisées par la forme de la modulation de fréquence) alors que les femelles isolées socialement ont des cris divergeant des autres individus [167, 168], et ce sans lien avec leur degré d'apparentement génétique [168]. De plus, le répertoire d'une femelle (i.e. la structure acoustique et le nombre de ses variantes) et l'identité de ses partenaires de partage vocal évoluent au cours du temps, en parallèle de la dynamique de ses affinités au sein du groupe social [76], et ce degré de variabilité acoustique est perçu par les congénères puisqu'ils répondent différemment à une variante présente, une variante

passée et une variante inconnue [102]. D'autres cas de convergence de certains paramètres acoustiques entre membres d'un même groupe social ont été observés suite à une perturbation sociale. Ainsi, lors de la formation de nouveaux groupes sociaux, on a pu constater un ajustement des paramètres acoustiques des cris d'un individu en fonction de ceux de son nouveau partenaire [169–171], en parallèle d'une augmentation de l'activité vocale [172], et plus particulièrement une augmentation de la fréquence des échanges vocaux [173–175], qui pourrait faciliter l'ajustement vocal au nouveau partenaire ainsi que la mise en place des relations sociales.

Enfin, l'individu émetteur va également pouvoir donner des informations relatives à son rôle social au sein du groupe par l'intermédiaire de son activité vocale. Le statut social d'un individu est notamment fonction de son sexe, et des différences entre singes mâles et femelles d'un point de vue vocal ont pu être mises en évidence. Qu'elles soient de l'ordre d'une phonation particulière ou de types de cris propres à un sexe, ces différences ont généralement été expliquées par des différences morphologiques et physiologiques [27, 77, 176]. Or dans le cadre d'une approche expérimentale, des mâles se sont révélés capables de produire des cris dits spécifiques aux femelles suite à une stimulation électrique cérébrale [177, 178]. En outre, dans un contexte de perturbation sociale [179, 180] ou de danger imminent [61, 181], des observations anecdotiques ont été faites de femelles produisant des cris dits spécifiques au mâle, lorsque celui-ci était absent ou bien demeurait anormalement silencieux. Le dimorphisme vocal observé refléterait donc l'utilisation préférentielle de certains types de cris par les individus, en fonction de leur rôle social (i.e. protection du groupe pour les mâles adultes versus maintien de la cohésion sociale intra-groupe pour les femelles adultes) [95, 178, 181, 182], plutôt que l'incapacité des individus d'un sexe à produire certains types de cris. Le rang hiérarchique est une autre information relative au statut social de l'individu qui peut transparaître dans la structure acoustique de ses cris [78], ou dans leur utilisation que ce soit en termes de fréquence d'émission [183] ou d'émission de types de cris particuliers [70, 184]. Il est intéressant de noter qu'en cas de changement de statut hiérarchique, on observe un ajustement des paramètres acoustiques [78] ou une apparition/disparation des types de cris spécifiques [70] de telle manière que le message contenu dans les signaux vocaux de l'individu émetteur demeure fiable. Il a d'ailleurs été démontré expérimentalement que cette flexibilité acoustique est perçue et utilisée par les congénères mâles pour évaluer le statut de leur adversaire et ajuster leur réponse [185].

En conclusion, chez les primates non humains comme chez l'homme, l'identité sociale et personnelle transparaissent dans le comportement

vocal sous différentes formes, que ce soit en termes de phonation ou d'utilisation d'un vocabulaire particulier. Néanmoins, chez les singes, seuls certains types de cris sont affectés, et du fait de la taille restreinte de leur répertoire vocal, les phénomènes sont de moindre ampleur que ceux observés chez l'homme dont le discours dans son ensemble fait preuve de plasticité.

6 Effet d'audience et règles d'interaction vocale

Chez l'homme, la communication est intentionnelle et directionnelle, visant une audience ou un interlocuteur particulier avec la volonté de lui communiquer un message. Le discours est par exemple modulé en fonction du public visé [50]. On constate l'existence d'interlocuteurs préférentiels, plus familiers [186] ou plus âgés [187–189]. Les conversations sont caractérisées par le respect de règles temporelles telle que le respect d'un délai de réponse (i.e. couper la parole est considéré comme impoli [189]) et l'organisation en tours de parole (i.e. on parle en alternance) [6, 190, 191]. On observe également des phénomènes de persistance (i.e. répétition du message jusqu'à obtention d'une réponse) et d'élaboration (i.e. modification de la structure acoustique) du signal destinés augmenter les chances de succès à poursuivre la conversation [192–194]. Enfin, l'homme est capable d'ajuster sa distance sociale à l'interlocuteur au cours de la conversation grâce à un phénomène de convergence/divergence langagière, phénomène qualifié d'accommodation vocale [195].

Outre son propre statut social, de récentes études chez les primates non humains ont mis en évidence qu'un individu était capable d'ajuster son comportement vocal en fonction de son auditoire, qu'il soit composé de receveurs passifs ou d'interlocuteurs vocalement actifs. Un premier ensemble de travaux a trait à ce qui a été qualifié d'effet audience, c'est-à-dire que l'émission de cris va dépendre de la présence de congénères à proximité. Ainsi, l'identité de ces receveurs potentiels va influer sur le comportement vocal de l'émetteur qui va choisir de ne vocaliser que lorsque certains partenaires sont présents. Dans le cas des cris d'alarme, l'émission d'un signal vocal augmentant le risque de se faire détecter par le prédateur, un individu a tout intérêt à en limiter la production. Aussi, les mâles vervets émettent plus fréquemment des cris d'alarmes si une femelle est à proximité, tandis que les femelles en émettent préférentiellement si des juvéniles sont à proximité [64]. Chez les chimpanzés et les bonobos, l'émission de cris de fonctions diverses par les mâles (cris alimentaires, cris de cohésion lors des déplacements) et les femelles (cris de copulation, cris de salutation envers les mâles dominants) est favorisée ou inhibée par le nombre et le statut des congénères présents (e.g. dominants *versus* subordonnés, partenaires

sociaux préférentiels), mais aussi par l'absence de certains (e.g. dominants) [183, 196–199]. Outre l'identité des partenaires présents, l'individu émetteur va également ajuster son comportement vocal en fonction de la distance le séparant de son audience : choisir de vocaliser ou non [56, 200, 201], ou bien sélectionner le type de cri acoustiquement approprié à une communication courte- *versus* longue-distance [202]. Enfin, plusieurs études ont révélé que les primates non humains étaient capables d'ajuster leur comportement vocal de manière encore plus complexe d'un point de vue cognitif. Les chimpanzés émettent différents sous-types de cris de détresse en fonction de l'intensité de l'agression ou du statut hiérarchique de l'opposant, mais ils utilisent également ces sous-types de cris stratégiquement : les victimes d'attaques sévères exagèrent la gravité de l'agression qu'elles subissent (en produisant des cris de détresse plus longs et plus aigus, caractéristiques d'agressions extrêmement sévères) si au moins un congénère dans l'audience est de rang égal ou supérieur à l'agresseur [203]. Les cercopithèques à diadème mâles émettent plus de cris d'alarme lorsque les membres de leur groupe sont proches d'un prédateur que lorsqu'ils en sont éloignés, et ce indépendamment de leur propre proximité vis-à-vis du danger [204]. Chez les chimpanzés, la probabilité qu'un cri d'alarme soit émis est plus élevée si l'individu se trouve en présence de congénères qui ignorent le danger (i.e. qui n'ont pas repéré par eux-mêmes la source du danger, ou qui n'ont pas encore eu l'opportunité d'entendre un cri d'alarme) *versus* des congénères qui sont déjà en possession de cette information [205, 206]. En outre, lors de la manifestation de ce comportement, l'individu adapte sa position spatiale de manière à signaler physiquement la position du danger (e.g. un serpent) et surveille visuellement ses congénères en alternant le regard entre le danger et ses congénères [207].

Un second ensemble de travaux a trait aux caractéristiques des échanges vocaux chez les primates non humains, apparentés à des formes simples de conversations selon plusieurs auteurs puisqu'ils sont caractérisés par le respect d'un certain nombre de règles d'interaction [208–210]. Une première règle temporelle correspond à l'évitement de la superposition des cris (i.e. éviter de se « couper la parole ») en respectant un délai de réponse. Le délai minimum limitant les risques de coupure est généralement de l'ordre de la durée moyenne d'un cri [211], tandis que le délai maximum de réponse assurant la continuité de l'échange vocal est chez la plupart des espèces de primates non humains de l'ordre de la seconde [212]. Il est intéressant de noter que ce délai de réponse peut être modulé en fonction de déterminants sociaux. Par exemple, un individu va répondre plus rapidement à un partenaire auquel il est plus affilié socialement [213]. Une seconde règle temporelle consiste à respecter des tours de paroles, c'est-à-dire à faire

en sorte que les deux interlocuteurs émettent leurs cris en alternance (et évitent de crier deux fois de suite) [148, 149, 211, 214]. Une autre règle, qualitative, a trait au fait que certains interlocuteurs vont être préférés. Ainsi, les aînés [149, 150, 211, 215] et les « amis » [16, 209, 213, 216] vont constituer des interlocuteurs préférentiels, recevant plus de réponses que les autres congénères. Enfin, il existe des règles ayant trait à la structure même des cris dont la modulation va permettre d'initier ou de prolonger un échange vocal. Les mâles chimpanzés sont ainsi capables de modifier la structure de leurs cris forts 'pant-hoots' (i.e. durée et nombre de certains éléments) afin de faciliter le développement d'un chorus avec un congénère (i.e. émission synchronisée, « en chœur », de cris) [217]. Un macaque est quant à lui capable de moduler son comportement vocal afin d'attirer l'attention d'un partenaire silencieux et d'augmenter la probabilité de recevoir une réponse en émettant de manière répétée des cris « exagérés » (i.e. augmentation de la modulation de fréquence, cris plus longs et plus aigus) [218]. Ces exemples attestent des capacités de persistance (répétition du message jusqu'à obtention d'une réponse) et d'élaboration (modification de la structure acoustique) chez les primates non humains [192–194]. Enfin, l'ajustement de la structure acoustique des cris peut aller jusqu'à copier l'interlocuteur vocalement. En effet, des études ont mis en évidence que dans le cadre d'un d'échange vocal, un individu est capable de sélectionner dans son répertoire le cri le plus proche structurellement de celui utilisé par son partenaire ; phénomène qui a été qualifié de « call matching » [219–221]. Chez les cercopithèques Diane, un phénomène de convergence/divergence acoustique inter-individuelle a même été décrit : les femelles émettent des cris très stéréotypés et individualisables lorsqu'elles se déplacent dans un habitat visuellement dense (besoin de cohésion spatiale) alors qu'elles convergent acoustiquement au cours d'un échange vocal (besoin de cohésion sociale) [219]. Ce phénomène est analogue au processus d'accommodation vocale chez l'homme [195].

La mise en évidence, chez les primates non humains, d'une certaine flexibilité dans l'utilisation des signaux vocaux en fonction du contexte social (modulation en fonction de l'audience ou de l'interlocuteur) a apporté la preuve du caractère intentionnel et directionnel de la communication vocale chez les primates non humains [206], des propriétés jusqu'il y a peu considérées comme étant l'apanage du langage humain. En outre, ces phénomènes apportent également des preuves supplémentaires, en contexte naturel, des capacités de contrôle moteur des vocalisations chez les singes. On retrouve chez les primates non humains des équivalents de nombreuses propriétés caractérisant la prise en compte de l'auditoire lors d'un discours et les conversations chez l'homme. Les différences homme-singes seraient donc, concernant

cet aspect du langage, clairement plus quantitatives que qualitatives. Tous ces parallèles sont particulièrement intéressants du fait du rôle clé qu'occupent les conversations dans le maintien et le renforcement des relations sociales chez l'homme [15], comme chez les singes [16].

7 Conclusion et réflexions évolutives

L'objectif de ce travail était de recenser un certain nombre de caractéristiques du langage humain dans une démarche comparative visant à déterminer les parallèles pouvant être tracés entre langage humain et communication vocale des primates non humains, ainsi que les limites devant être posées à ces comparaisons. Les capacités de contrôle de la production vocale chez l'homme sont nettement supérieures à celles des autres primates. Toutefois, l'analyse des structures anatomiques et neuronales sous-tendant cette aptitude a révélé des homologies structurales entre homme et singes, suggérant l'existence de différences quantitatives plus que qualitatives. Les singes sont capables de contrôler l'expression et de moduler leur signal vocal dans des paradigmes expérimentaux mais aussi en situation naturelle sociale (e.g. effet audience, règles conversationnelles), ce qui atteste d'un certain degré de contrôle moteur vocal, en plus d'apporter la preuve du caractère intentionnel et directionnel d'au moins certaines de leurs vocalisations.

D'autre part, si les parallèles homme-singes sur le plan de l'encodage d'informations émotionnelles et identitaires dans les vocalisations sont parmi les plus aisés à tracer, la limite à l'analogie reste difficile à fixer lorsque l'on aborde la question de la sémanticité. En effet, si les primates non humains possèdent des signaux référentiels avec un caractère sémantique avéré, on ne retrouve pas chez les singes la faculté de déplacement caractéristique du langage humain. En lien avec ceci, les capacités combinatoires complexes (e.g. variations systématiques du message par affixation ou combinaison d'éléments) récemment mises en évidence chez les primates non humains suggèrent des analogies plus poussées entre homme et animal que celles considérées auparavant, mais le degré de complexité des mécanismes cognitifs sous-tendant ces combinaisons chez les singes reste inconnu. La limite de l'analogie concernant la référentialité et les propriétés combinatoires semble donc ne pas se situer sur le plan de la production, mais plutôt sur le plan de la représentation et de l'intégration de ces signaux au niveau cognitif. Des études supplémentaires sont nécessaires avant de pouvoir déterminer avec certitude où se situe la limite à l'analogie.

Enfin, l'étude de la communication vocale chez les singes à travers le prisme de la vie sociale, qu'il s'agisse du développement vocal chez les jeunes ou de la flexibilité vocale chez l'adulte (encodage de l'identité sociale, ajustement à l'audience, règles conversationnelles), suggère de

nombreuses similitudes entre homme et animal. L'influence des partenaires sociaux est essentielle au développement et joue fortement sur l'utilisation des vocalisations tout au long de la vie des individus, chez l'homme comme chez les singes. Ici encore, les différences entre homme et animal semblent prendre une dimension essentiellement quantitative, sur le plan de la production d'une part (capacité phonatoires) et en termes de capacités cognitives (notamment d'apprentissage) d'autre part.

De manière globale, les divers travaux considérés dans cette revue corroborent l'idée d'une similarité entre langage et communication vocale des primates non humains, impliquant à la fois des analogies importantes (notamment sur le plan qualitatif) mais aussi des différences. Les différences décrites sont surtout d'ordre quantitatif (e.g. en termes de flexibilité de production et d'utilisation), mais aussi d'ordre qualitatif notamment sur le plan de la cognition (e.g. capacités d'abstraction, de représentation mentale, de générativité et de récursivité). Toutefois, des études de plus en plus nombreuses proposant des paradigmes expérimentaux de plus en plus pertinents pour les animaux révèlent des capacités cognitives jusqu'alors insoupçonnées. Par exemple, des expériences ont démontré que l'homme et les singes possèdent un système similaire de dénombrement d'unités perçues dans différentes modalités sensorielles [222], d'ordination [223] et d'addition de valeurs numériques [224].

S'il est difficile d'atteindre un consensus quant aux identités (sous-entendant une homologie d'un point de vue évolutif, soit une continuité évolutive : propriété présente chez deux taxons apparentés qui l'ont héritée d'un ancêtre commun) et aux différences partielles (analogies résultant d'une évolution convergente : apparition indépendante d'une même propriété dans deux taxons éloignés) ou majeures (résultant d'une évolution divergente : deux taxons éloignés présentent des propriétés distinctes) entre homme et animal, un consensus existe quant à l'existence d'une continuité dans la lignée évolutive ayant conduit jusqu'à l'homme actuel qui partage, de fait, un ancêtre commun avec les primates non humains. Le langage est un phénomène complexe qui ne peut être apparu *de novo* mais qui a au contraire, sans aucun doute, une longue histoire évolutive. Son évolution est probablement le fruit de pressions sélectives qui se sont exercées, et s'exercent aujourd'hui encore, sur la communication d'autres espèces. Les primates constituent un ordre extrêmement diversifié sur les plans morphologique, écologique, social, et communicatif notamment. Des études comparatives entre plusieurs espèces de primates non humains ont permis d'identifier plusieurs pressions de sélection majeures et les adaptations qu'elles ont engendrées. Les adaptations, sur le plan communicatif, peuvent avoir pour objet le système de communication (e.g. type et

nombre de cris du répertoire, modalité(s) sensorielle(s) impliquée(s)) ou bien la structure même des signaux (e.g. tonalité, durée, intensité, degré de variabilité des signaux).

L'habitat d'une espèce constitue une première force de sélection majeure qui favorise l'utilisation de certaines modalités sensorielles et conditionne la structure même des signaux (discrets *versus* gradués). Ainsi, les singes vivant en forêt tropicale, où les feuillages denses limitent la visibilité, utilisent plus la modalité acoustique que des espèces vivant en savane chez lesquelles on trouve des éléments de communication gestuelle par exemple [225–227]. De manière similaire, les espèces vivant dans des milieux dans lesquels la communication est malaisée (e.g. fort bruit de fond, dégradation du son, manque de visibilité) possèdent des signaux très distincts les uns des autres (i.e. répertoire discret) évitant la confusion de signaux proches structurellement [228].

La prédation constitue une seconde pression de sélection majeure sur l'évolution de la communication et de la cognition chez les primates non humains [229, 230]. Les animaux subissant des attaques de divers prédateurs, exigeant des réactions comportementales adaptées différentes, ont développé des cris référentiels pour signaler la nature du danger sous forme de cris simples, complexes ou de séquences [59, 60, 89, 231, 232]. De plus, la structure fine des signaux varie également en fonction des stratégies anti-prédatrices : les espèces cryptiques (i.e. discrètes) présentent des cris moins détectables (e.g. de faible intensité, de basse tonalité) et vocalisent moins souvent [233, 234].

Enfin, la vie sociale constitue un moteur clé de l'évolution de la communication chez l'animal. C'est particulièrement vrai chez les primates pour lesquels la communication joue un rôle essentiel dans la constitution et le maintien de liens sociaux forts entre les membres d'un groupe [15, 235]. La théorie d'une coévolution entre vie sociale et communication fait le postulat que le degré de complexité du système social d'une espèce est en lien avec la complexification de ses capacités communicatives [86, 236]. Plusieurs études sont venues corroborer cette théorie en démontrant que la taille du groupe social, sa composition, et la force du lien social entre les congénères influencent le degré de complexité du répertoire vocal (e.g. nombre de types de cris, existence de combinaisons, variabilité structurale des signaux) [86, 235–237], ainsi que le degré de sensibilité auditive des animaux [238]. En outre, plusieurs études portant sur d'autres modalités ont révélé une influence de la complexité sociale sur la complexité de la communication gestuelle (e.g. taille du répertoire de geste, complexité de la dynamique de communication) [239], faciale (e.g. taille du répertoire de mouvements faciaux) [240] et olfactive (e.g. complexité chimique des sécrétions glandulaires) [241], suggérant un lien fort et plus général entre socialité et communication.

Le fait que des pressions de sélection comparables s'appliquent à diverses modalités communicatives nous incite à étendre la comparaison homme-animal à la recherche de parallèles supplémentaires avec le langage humain. De nombreuses investigations se sont notamment portées sur la communication gestuelle des primates non humains, et ont démontré l'existence de caractéristiques similaires à celles du langage (voir [5] pour une revue) telles que la référentialité [242, 243], la sensibilité à l'audience et à son état attentionnel [5, 244, 245], l'intentionnalité [246, 247], une utilisation flexible [248, 249] pouvant être liée à un apprentissage [250], ainsi que des analogies neuronales et anatomiques entre homme et primates non humains quant à la production de gestes communicatifs [251, 252]. Ainsi, de plus en plus de spécialistes proposent d'adopter une approche multimodale de la communication afin d'évaluer de manière plus exhaustive les différents facteurs et mécanismes impliqués dans son évolution [253–256].

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DES COMBINAISONS VOCALES DANS LA COMMUNICATION DE CERCOPITHEQUES FORESTIERS

Il est classiquement admis que les études comparatives sur la communication des animaux peuvent permettre de mieux comprendre la coévolution de la vie sociale, de la communication vocale et des capacités cognitives, notamment l'émergence de certaines propriétés du langage humain. De récentes études ont suggéré la présence de capacités combinatoires chez les primates non humains, capacités qui permettraient à ces animaux de diversifier leurs répertoires ou d'enrichir les messages transmis par leurs vocalisations en dépit de capacités articulatoires limitées. Toutefois, les fonctions des cris combinés et les informations qui en sont extraites par les receveurs restent méconnues. Cette thèse porte sur les capacités de combinaison vocale de cercopithèques forestiers sauvages : la mone de Campbell (*Cercopithecus Campbelli*) et le singe Diane (*Cercopithecus Diana*). Premièrement, à l'aide d'expériences de repasse acoustiques, j'ai étudié la nature combinatoire de cris combinés et les informations qui en sont extraites par les receveurs chez ces deux espèces. Les résultats ont confirmé chez les mâles mone de Campbell la présence d'un mécanisme de suffixation diminuant l'urgence du danger signalé par un cri d'alarme ainsi que, chez les femelles singe Diane, la présence de cris complexes combinant linéairement les messages des deux unités qui les composent, signalant respectivement l'émotion et l'identité de l'émetteur. Deuxièmement, une étude observationnelle du contexte d'émission de cris simples et combinés par des femelles mones de Campbell sauvages a révélé une utilisation flexible de la combinaison en fonction du besoin immédiat de rester discret (*i.e.* cris simples) ou de signaler son identité (*i.e.* cris combinés). Finalement, j'ai comparé les systèmes de communication des femelles de ces deux espèces pour identifier leurs points communs et leurs différences. Leurs répertoires sont basés principalement sur des structures acoustiques homologues, comme prédit par leur proximité phylogénétique. Cependant, les femelles de ces deux espèces diffèrent fortement dans leur utilisation de ces structures. Par exemple, le grand nombre de cris combinés chez les singes Diane semble permettre un accroissement considérable de leur répertoire vocal par rapport aux mones de Campbell. Etant donné l'organisation non-aléatoire de ces combinaisons vocales qui font sens pour les receveurs et de leur utilisation flexible en fonction du contexte, je propose un parallèle avec une forme simple de morphosyntaxe sémantique et discute aussi plus généralement de la possibilité de trouver des capacités similaires chez d'autres espèces animales.

VOCAL COMBINATIONS IN GUENON COMMUNICATION

It is generally accepted that comparative studies on animal communication can provide insights into the coevolution of social life, vocal communication, cognitive capacities and notably the emergence of some human language features. Recent studies suggested that non-human primates possess combinatorial abilities that may allow a diversification of vocal repertoires or a richer communication in spite of limited articulatory capacities. However, the functions of combined calls and the information that receivers can extract remain poorly understood. This thesis investigated call combination systems in two species of guenons: Campbell's monkey (*Cercopithecus Campbelli*) and Diana monkey (*Cercopithecus Diana*). Firstly, I studied the combinatorial structure and relevance to receivers of combined calls in of both species using playback experiments. Results confirmed the presence of a suffixation mechanism reducing the emergency of danger signaled by calls of male Campbell's monkeys. Also, they showed that combined calls of females Diana monkeys convey linearly information via their two units, which signal respectively caller's emotional state and identity. Secondly, focusing on the context associated with the emission of simple and combined female Campbell's monkey calls, results revealed flexible use of combination reflecting the immediate need to remain cryptic (i.e. simple calls) or to signal caller's identity (i.e. combined calls). Finally, I compared females' communication systems of both species to identify their similarities and differences. As predicted by their close phylogenetic relatedness, their repertoires are mostly based on homologous structures. However, the females differ strongly in their use of those structures. In particular, the great number of calls combined by Diana monkeys increases considerably their vocal repertoire compared to Campbell's monkeys. Given that the combinations are non-random, meaningful to receivers and used flexibly with the context, I propose a parallel with a rudimentary form of semantic morphosyntax and discuss more generally the possible existence of similar capacities in other non-human animals.